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A morphological study of the genus *Penthalodes* (Acari, Prostigmata, Eupodoidea, Penthalodidae) with description of a new species

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Abstract

The morphology of representative species of the genus *Penthalodes* is reviewed. A new generic diagnosis and an identification key for adults of *Penthalodes* species is provided. Previous descriptions of *Penthalodes ovalis* from Alaska and Hawaii are considered as different species and named as *P. alaskaensis* (Strandtmann) **sp. n.** and *P. hawaiiensis* (Strandtman & Goff) **sp. n.**, respectively. *Penthalodes polonicus* **sp. n**. is described and illustrated based on material collected in Poland.

Key words: taxonomy, identification key, morphological review, morphological description

Introduction

The genus *Penthalodes* Murray, 1877 has as its type species *Megamerus ovalis* Dugés, 1834, collected from an unknown European locality. Subsequent to Dugés description Koch (1838) described the same species as *Penthaleus ovatus*. Murray (1877) transferred the type species into the section Eupodidae, instead of the Trombidiidae, where Dugés placed it. Moreover, due to the lack of a line which separates the "thorax" and "abdomen", he stated that it cannot be placed in the genus *Penthaleus* (referring to Koch's description), but in a new genus *Penthalodes*. He also formulated a new name for the species, *Penthalodes ovalis*.

Thor and Willmann's (1941) monograph on the Prostigmata provided the first review of *Penthalodes*. They gave an extensive description of the type species, viz. *Penthalodes (Megamerus*) *ovalis* (Dugés, 1834). The descriptions of another two species, *P. columbiae* Berlese, 1921 and *P. inflatus* Dugés, 1834 they considered very superficial; *P. inflatus* was recognized as *species enquirenda*. The latter has linopodes-like front legs and is probably not a *Penthalodes* species (Strandtmann 1971).

Unfortunately, it is impossible to identify species according to these descriptions. Since Thor and Willmann (1941), four following species are currently recognised. Dr Edward Baker (1946) described three new species from North and Central America, which were distinguished by the shape of the epirostrum and idiosomal setae and ornamentation. Shiba (1978) described a new species from Japan, which is easily diagnosed by the epirostrum and rhagidial organs of tarsi I and II.

Two additional studies gave further data regarding *P. ovalis* (Strandtmann 1971; Strandtmann & Goff 1978). However, specimens of *P. ovalis* on original microscope slide preparations from Hawaii, earlier examined by Strandtmann and Goff, are now damaged (spoiled) or hardly visible. Dr Anne Baker (1987, 1990) presented selected morphological details for an undescribed *Penthalodes* sp. and *P. ovalis*. Strandtmann (1971, 1974) prepared a brief key for determination and check list of *Penthalodes* species, including synonyms. Most recently, Kaluz (2000) provided an extensive redescription of *P. ovalis* from material collected in Slovakia and Turkey.

Earlier descriptions of *P. ovalis* from Alaska (Strandtmann 1971) and Hawaii (Strandtmann & Goff 1978) show substantial morphological differences in the solenidia of rhagidial organs I and II and epirostra. These

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important diagnostic features strongly suggest these specimens represent two different species, not morphological forms resulting from intraspecific variability, and are herein described as new. This dissimilarity of *P. ovalis* from Alaska and Hawaii was observed by Strandtmann (1971) and later Kaluz (2000), but not discussed. Both authors supposed that *P. ovalis* has a circumpolar distribution and regarded the morphological differences as intraspecific.

Kaluz (2000) redescribed *P. ovalis* based on European specimens. Unfortunately, the original type material no longer exists, so cannot be verified. However, many other specimens of *P. ovalis* collected in Europe do not match the redescription of Kaluz (2000). There exists morphological diversity among specimens originating from different parts of Europe, e.g. from Poland and Spain (personal observations). Even specimens originating from various parts of Poland differ in characteristics of their epirostra or pedipalpal tarsi. Therefore, we can assume they are most probably different species or subspecies.

This paper presents the morphology of specimens collected in the Polish Tatra Mountains. Due to morphological differences of known *Penthalodes* species, especially *P. ovalis*, the specimens of this study area are recognized as a new species. An identification key to species of *Penthalodes* is included as well as an extensive discussion on morphological diversification among *Penthalodes* representatives. Finally, a new generic diagnosis is provided, as well as new names and species diagnoses for the collections of *P. ovalis* from Alaska and Hawaii.

Material and methods

Mites were collected by extraction in Tullgren apparatus and stored in 75% ethanol. Some specimens were embedded in Faure's liquid on permanent microscopic slide preparations, while others were observed in lactic acid. However, they were first placed in 5% potassium hydroxide (KOH) for a short time to dissolve uric acid deposits. For comparison, representatives of *Penthalodes* from Hawaii (courtesy of the Bishop Museum in Honolulu), were also used. Observations and illustrations were made using a standard light microscope equipped with a phase-contrast optical system and immersion objective. All illustrations are original. All measurements are given in micrometers (μm). Division of the body into aspidosoma, podosoma and opisthosoma is taken after Grandjean (1969) and modified by the author (Jesionowska 1996, 2000, 2003). The term "filiform" is used for setae *bo* only (Jesionowska 2002). The abbreviation for furrow "das" is derived from the three furrows, i.e. disjugal, abjugal and sejugal, which meet dorsally and separates the prodorsum from the opisthosoma. Notations for the prodorsal setae are: *ro* (=v_1, *iv*) - rostral; *bo* (=sc_1, *T*) - bothridial; *le* (=v_2, *ev*) - lamellar; *xa* (=sc_2, *sc*) - anterior exobothridial. Abbreviations for pedipalp and leg articles: Cx – coxal region, Tr – trochanter, FG – femorogenu, G – genu, Tb – tibia, Ts – tarsus. Nomenclature for pedipalpal tarsal setae is according to Jesionowska (1991). Morphological considerations are based on original descriptions of the following *Penthalodes* species: (1) *P. boneti* (Baker 1946), (2) *P. oregonensis* (Baker 1946), (3) *P. turneri* (Baker 1946), (4) *P. carinatus* (Shiba 1978), (5) *P. ovalis* from Alaska (Strandtmann 1971), (6) *P. ovalis* from Hawaii (Strandtmann & Goff 1978) and (7) *P. ovalis* sensu Kaluz (2000), as well as some data from *P.* species and *P. ovalis* given in the papers of Dr Anne Baker (1987, 1990).

Results

Genus *Penthalodes* Murray, 1877

Type species: *Megamerus ovalis* Dugés, 1834
Synonym: *Penthalodes ovalis*: Murray (1877)

Diagnosis. Adults with characteristic epirostrum overhanging the gnathosoma. Epirostrum without connection with naso. Naso smooth, spherical, half hidden in a small cavity of prodorsal wall. Setae *ro* on naso, tiny, nude, not branched. Idiosoma angular, with moderate sclerotization of integument and

characteristic reticulate ornamentation formed mainly by pentagons or pentagons and hexagons. Dorsum with two furrows in the form of the letter "V". Idiosoma (excluding podosoma and genital region) with 13 pairs of setae, of which nine pairs belong to the opisthosoma. One pair of anal setae (*an*) flank anal cleft only. Legs shorter than idiosoma. All tibiae and genua with solenidia. Tibia I and II each with two solenidia, proximal solenidion erect, distal solenidion recumbent in depression. Genua with one erect solenidion each. Genua I and II each with one famulus inserted near distal margin. Hypostome consists of a proximal rectangular and distal triangular part.

Key to species of *Penthalodes*

1 Epirostrum trilobed 2
- Epirostrum monolobed 5
2 Middle part of epirostrum triangular 3
- Middle part of epirostrum pentagonal, sharply tipped. Lateral lobes distinctly formed, asymmetrically tongue-shaped with tips oriented antiaxially. Ornament of epirostrum reticulate. Alaska ..... *P. alaskaensis* (Strandtmann, 1971) **sp. n.**
3 Lateral lobes of epirostrum weakly formed. Rhagidial organ I with two banana-shaped or baculiform solenidia in tandem, in confluent depressions 4
- Lateral lobes of epirostrum distinctly formed, tongue-shaped, oriented obliquely in relation to middle lobe. Rhagidial organ I with two lanceolate solenidia in tandem, each in separate depression. Slovakia and Turkey ..... *P. ovalis* (Dugés) sensu Kaluz, 2000
4 Lateral lobes of epirostrum small, triangular, pointed. Ornament of epirostrum reticulate. Opisthosomal setae (excluding genital region) loosely feathered. Hawaii ..... *P. hawaiiensis* (Strandtman & Goff, 1978) **sp. n.**
- Lateral lobes of epirostrum large broadly rounded. Ornament of epirostrum irregular, punctate, consisting of large and tiny costulae. Opisthosomal setae (except for genital region) tridactylate. Poland ..... *P. polonicus* **sp. n.**
5 Epirostrum a broadly rounded lobe distally, its ornament sparsely punctate posteriorly, and anteriorly with fine hairs. USA, Oregon ..... *P. oregonensis* Baker, 1946
- Epirostrum differently shaped 6
6 Epirostrum triangular 7
- Epirostrum right-angled trapezium shaped in proximal part with slightly pointed lateral cusps, and in middle part transforms into short tongue-shaped process. Ornament of epirostrum reticulate posteriorly and striate in tongue-shaped part. Mexico ..... *P. boneti* Baker, 1946
7 Lateral edges of epirostrum plicate, with at least two folds each, ornamentation reticulate. Rhagidial organ II with three solenidia, each in separate depressions, two of which are parallel and positioned distally. Japan ..... *P. carinatus* Shiba, 1978
- Lateral edges of epirostrum straight, without lateral folds, ornamentation reticulate posteriorly and striate anteriorly. Rhagidial organ II with three solenidia, in line. USA, Texas ..... *P. turneri* Baker, 1946

Taxonomy

Morphological differences evident in two descriptions of *P. ovalis* sensu lato, i.e. *P. ovalis* sensu Strandtmann (1971) from Alaska, sensu Strandtmann & Goff (1978) from Hawaii, both indicate they are different species. Consequently, these two species from Alaska and Hawaii are re-named and their diagnoses refined. Specimens from Slovakia and Turkey are designated as species for new redescription of *Penthalodes ovalis* because, according to Kaluz (2000) they derive from Europe like the type material. These specimens, however, may be also thought to be new, but these are not designated as a new species pending a review of European *Penthalodes*. Additionally, a new species from Poland is described.

***Penthalodes alaskaensis* n. sp.**

Synonym: *P. ovalis* Strandtmann, 1971, *Pacific Insects* 13, 1, 75–118
Locus typicus: Northern Alaska, tundra samples

Diagnosis. Epirostrum trilobed, middle part pentagon-shaped, with wide base and sharp, triangular tip; lateral lobes narrow, parallel to middle part, in greater part fused with it. Free parts of lateral lobes tongue-shaped with sharp tips directed antiaxially. Ornament of epirostrum reticulate. Dorsal idiosomal setae, except setae *ro* and *bo*, plumose. Rhagidial organ I with two recumbent baculiform solenidia, in tandem lying in confluent depressions. Stellate famulus subtending rhagidial organ I. Rhagidial organ II with three recumbent baculiform solenidia lying in tandem in confluent depressions. Solenidia of rhagidial organ I and two proximal solenidia of rhagidial organ II equal in size. Longest solenidion is the third distal solenidion of rhagidial organ II.

For the original description and deposition of type specimens see Strandtmann (1971).

***Penthalodes hawaiiensis* n. sp.**

Synonym: *P. ovalis* Strandtmann & Goff, 1978, *Pacific Insects* 19, 3–4, 121–143.
Locus typicus: Hawaii, vicinity of Volcano-Hilo road, samples from grass, lichen, treefern forest, cane fields

Diagnosis. Epirostrum trilobed; middle part of epirostrum large, triangular; lateral lobes weakly developed with slightly pointed, resembling triangles. Dorsal idiosomal setae, except setae *ro* and *bo*, loosely feathered. Rhagidial organ I with two recumbent baculiform solenidia, in tandem, in confluent depressions and one tiny spatulate solenidion in separate pit inserted laterally antiaxially in relation to rhagidial organ I. Famulus absent. Rhagidial organ II with three recumbent baculiform solenidia, staggered, in confluent depressions. Solenidia of rhagidial organ II of unequal size, not overlapping each other.

For the original description and deposition of type specimens see Strandtmann and Goff (1978).

***Penthalodes polonicus* n. sp**.
(Figs 1–7)

Diagnosis. Epirostrum trilobed, lateral lobes broadly rounded; in lateral view, base of epirostrum sloping; without reticulation. Dorsal idiosomal setae, except setae *ro* and *bo*, tridactylate, with short stem. Rhagidial organ of tarsus I with two banana-shaped solenidia in tandem in a confluent depressions and one T-shaped solenidion in a separate pit inserted laterally to proximal solenidion. Small stellate famulus inserted laterally on mid-region of tarsus I, well separated from rhagidial organ. Rhagidial organ of tarsus II with three thin baculiform solenidia, in tandem, in a common depression with the distal part of each solenidion overlapping the preceding one. One, small spine-like solenidion (possibly a famulus) inserted in pit laterally to rhagidial organ II, at the level of proximal solenidion.

Description. Body with well developed ornamentation, moderately sclerotized. Idiosoma angular (Fig. 3) with ornamental costulae forming pentagons (i.e. reticulate pattern). Dorsum with two “V”-shaped furrows. Idiosomal length (excluding epirostrum) about 400 µm, width (at the level of setae c_2) about 250 µm. Legs shorter than idiosoma. Ratio of idiosomal length to leg I length: 1:15.

Aspidosoma. (Figs 1, 2, 3C, D) Prodorsum forms a steep anterior wall of idiosoma. Ornamentation consists of large tear-shaped costulae (i.e. point-shaped with tiny spine) and minute costulae discernible as dots. Large costulae form pentagons, while minute costulae form parallel lines on the surface of each pentagon. Naso small, smooth, and spherical, with one hemisphere hidden in a cavity. Epirostrum trilobed with lateral lobes broadly rounded, distinctly shorter than medial lobe (Figs 3CD). Four pairs of prodorsal setae: *ro*, *bo*, *le*, *xa* (about 6, 56, 37 and 25 long, respectively). Setae *ro* tiny, nude, inserted on frontal surface of naso, adjacent in a common depression (possibly a result of slide-mounting). Setae *bo* filiform, inserted on prodorsum in deep bothridia dorsally; setae *le* and *xa* situated frontally. Setae *le* and *xa* tridactylate with short basal branches. V-shaped furrows start lateral to setae *bo*. Transverse furrow separating prodorsum from opisthosoma absent.

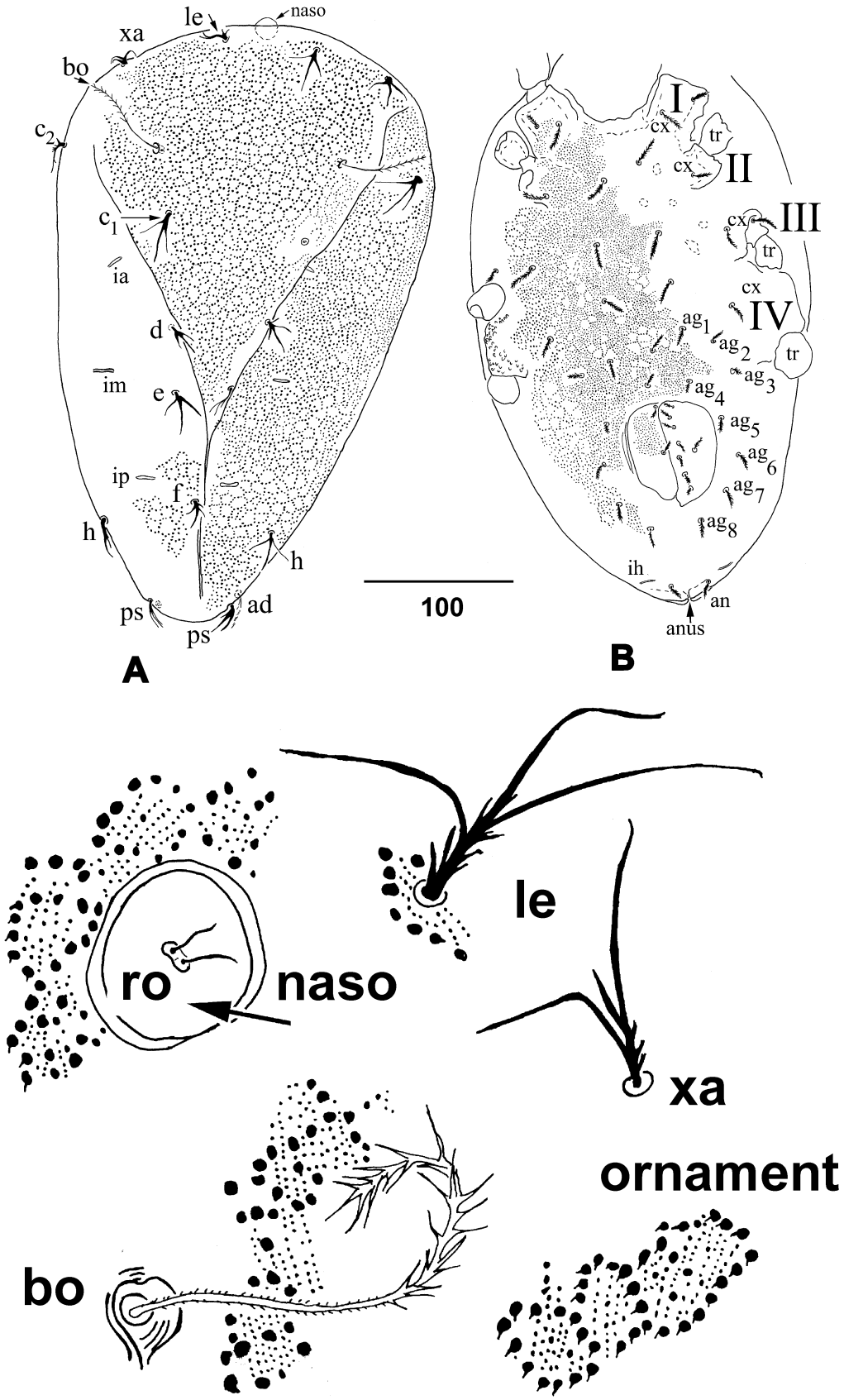

FIGURE 1. *Penthalodes polonicus* **n. sp.** Female. (A) Dorsum; prodorsal setae: *ro*, *le*, *bo*, *xa*; opisthosomal setae: c_1, c_2, *d*, *e*, *f*, *h*, *ps*, *ad*. Lyrifissures: ia, im, ip, ih. (B) Venter; coxal regions: cx 1–4; trochanter: tr 1–4; aggenital setae: ag 1–8; anal setae: *an*.

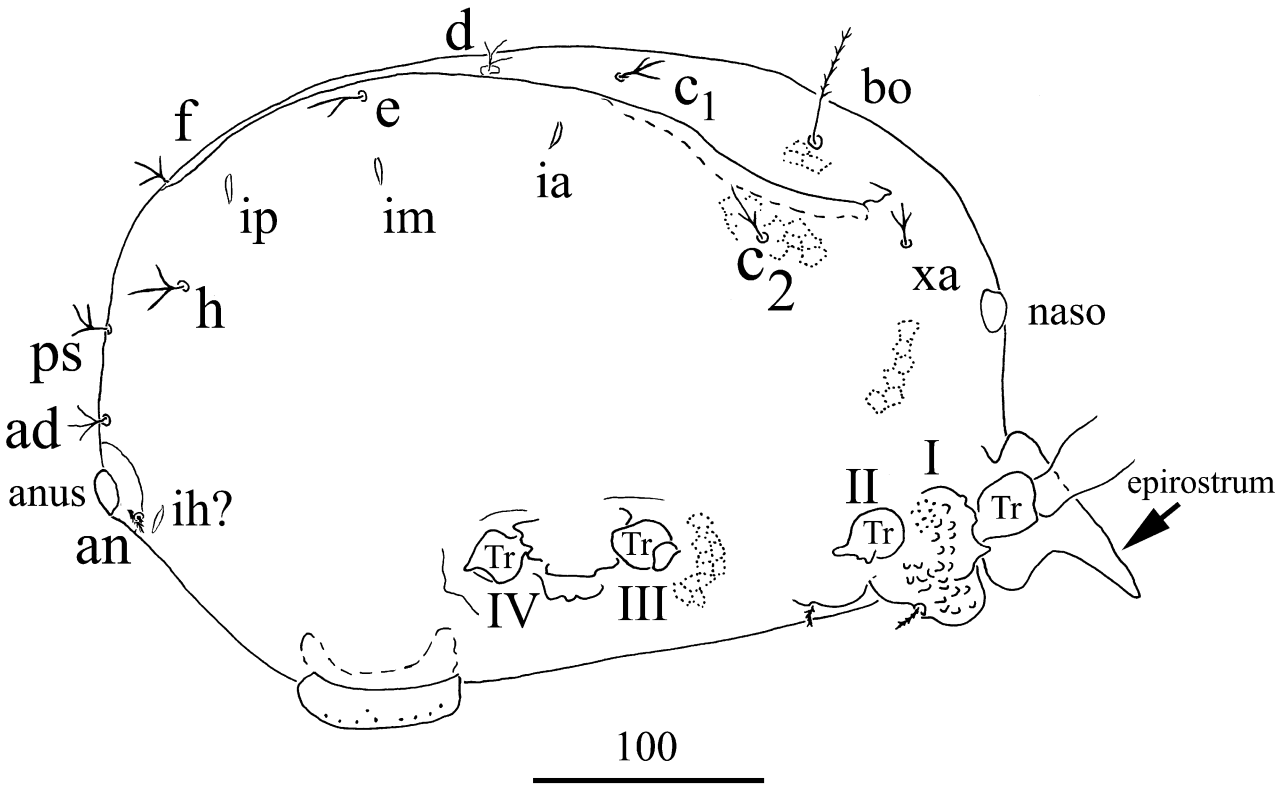

FIGURE 2. *Penthalodes polonicus* **n. sp.** Female. Idiosoma, lateral view.

Gnathosoma (Figs 3AB, 4). Subcapitulum (Fig. 4AB) about 110 long, conical, with well developed ornamentation comprising spine- to point-shaped costulae on smooth integument. Lateral lips (LL) connected by a smooth membrane dorsally for approximately two thirds their total length. Ventrally, the free parts of lateral lips bear one pair of setae *n*, inserted slightly distal to labial apex; and one pair of setae *m* latero-basally. Setae *n* and *m* plumose with long outgrowths. On ventral side, lateral lips fused to hypostome (H), delimited by sclerites *sc*. Top of hypostome forms small labium (LI). Hypostome divided by inner sclerite into a basal rectangular and distal triangular part. Paraxial surfaces of free part of lateral lips, as well as the ventral part of labrum (LB), strongly sclerotized. Distal antiaxial parts of lateral lips smooth and plicate. Adoral setae difficult to discern. Free part of labrum not longer than those of lateral lips. Chelicera (Fig. 3AB) about 115 long, elongated, ornamented with tiny spines. Cheliceral seta absent. Fixed digit hood-shaped, distally bifurcate covering most of movable digit. Movable digit strongly sclerotized, narrows distally into hooked claw. Pedipalps (Fig. 4CD) four-segmented, Tr-FG-Tb-Ts; coxal regions well formed and fused partially with dorso-basal subcapitulum (Fig. 4B). Pedipalp about 166 long, Tr to Ts: 25-55-57-29. Number of setae and solenidia: 0-2-3-9(1). Setae on femorogenu (d_1-15, d_2-21 long) and tibia (d_1-18, *lt*-11, d_2-13 long) plumose. Seta d_2 on FG with a very long terminal spine. Pedipalpal tarsus elongated, sharply tipped, linear in profile with nine setae and one recumbent solenidion in depression dorsally; seta *acmg* (=*d*; 10 long) thick, pilose, angled basally, the largest; seta *cm*' (11 long) positioned paraxially, almost smooth, spiralled; seta *ul*" slightly thickened, shortly pilose; setae *ul*', *u*" and *u*' (5 long each) cylindrical, hollow, each terminating in strong sclerotized solid (black) carina; seta *a* (7 long), thickened, with distal spine; setae *s* plumose, *la*" pilose, very short (3 and 4 long, respectively). Ventro-distal part of tibia terminating in distinct spine-like process.

Opisthosoma (Figs 1, 2; Table 1). Opisthosoma with characteristic "V"-shaped furrows, lacking any transverse furrows (as "das" or disjugal furrow). Ornamentation same as prodorsum, i.e. tear-shaped costulae forming pentagons, each covered by minute point-shaped costulae forming parallel lines (Fig. 1). Ornamentation on opisthosoma venter more delicate, with costulae being visibly smaller than dorsal costulae.

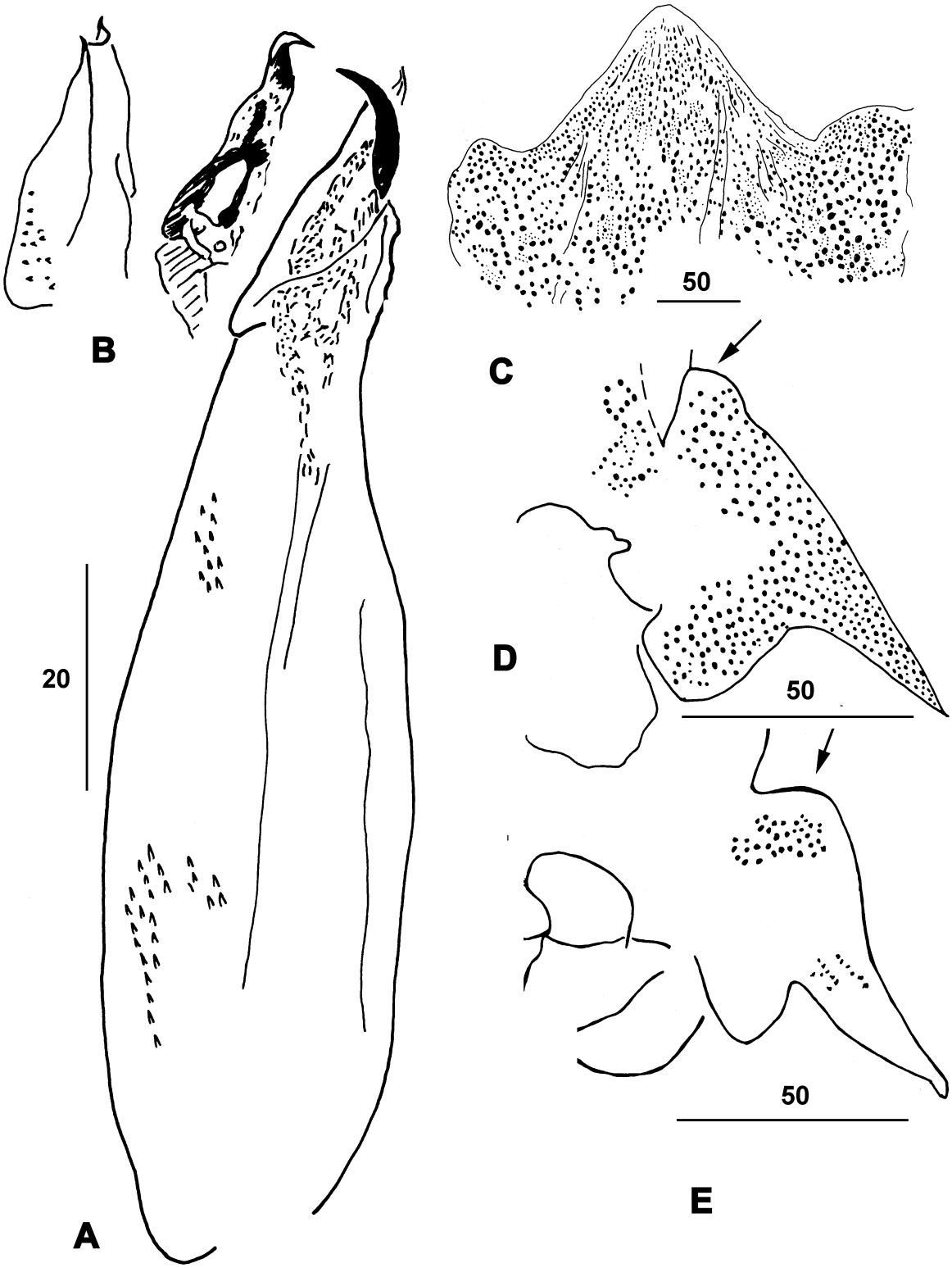

FIGURE 3. *Penthalodes polonicus* **n. sp.** Female. (A) chelicera, lateral view. (B) cheliceral digits in detail. (C) epirostrum, dorsal view. (D) epirostrum, lateral view. (E) *Penthalodes* sp., epirostrum, lateral view.

Opisthosoma composed of nine fused segments: C, D, E, F, H, PS, AD, AN, PE. Segment C with two pairs of setae c_1 and c_2; c_2 inserted slightly distad of c_1, almost at the level of setae *bo*. Segments D to AN with one pair of setae each, i.e., *d*, e, *f*, *h*, *ps*, *ad* and *an*, respectively. Segments H to PE form the posterior wall of the opisthosoma which is steep, beginning at about the level of setae *h* (Fig. 2). Distances between insertions of

setae *ps-ad*, *ad-an* are almost equal and rows of these setae arranged one under another; setae *ad* well distant of anal cleft, hence the anal cleft is accompanied by only one pair of setae, *an*. Setal pair *f* aligned with lyrifissures *ip*. Setae *h* are inserted laterally and well posterior to setae *f* and lyrifissures *ip*. V-furrows end about at the level of setae *f*. Distances between insertions of opisthosomal setae distinctly longer than length of setae. Opisthosomal setae *c* to *ad* tridactylate with short stem, and prominent medial "dactyl". With four pairs of lyrifissures (*ia*, *im*, *ip*, *ih*?), slit-like with strong sclerotized margins. Anal cleft very short, positioned terminally. Anal valves well developed, inserted on a small protuberance of segment PE. Setae *an* plumose, close to anterior margin of PE, similar to genital setae.

TABLE 1. Homology of opisthosomal setae in representatives of the family Penthalodidae.

Names of setae according to Strandtmann 1967, 1971	*Stereotydeus* with new proposition for this taxon	*Protopenthalodes* Jesionowska, 1989	*Penthalodes* according to Baker 1987	*Penthalodes* according to Kaluz 2000	*Penthalodes* new proposition
i.h. (internal humeral)	present; (c_1)	present	c_1	c_1	c_1
e.h. (external humeral)	present; (c_2)	present	c_2	sc	c_2
d_1 (first dorsal)	present; (d)	absent	d_1	d_1	-
d_2 (second dorsal)	present; (e)	present	e_1	e_1	d
i.l. (internal lumbar)	present; (f)	present	f_1	f_1	e
e.l. (external lumbar)	present; (h)	absent	f_2	f_2	-
i.s. (internal sacral)	present; (ps_1)	present	absent	h_1	f
e.s. (external sacral)	present; (ps_2)	present	absent	absent	h
a_3 (anal seta No 3) or a_1	present;(ad_1)	present	ps_1	ps	ps
a_2 (anal seta No 2)	present; (ad_2)	present	ps_2	ps	ad
a_1 (anal seta No 1) or a_3	present; (an)	present	ps_3	absent	an

Genital region (Figs 1B, 5; Table 2). Costulae forming pentagons and irregular lines or points, distinctly smaller and not as homogenous as those on dorsum. Reticulation distinct in pregenital area, but punctate in lateral aggenital region. Genital valves strongly sclerotized, well separated from aggenital region, differently ornamented with irregular tiny spines. Between coxal regions IV and genital valves (pregenital area) eight aggenital setae form two alignments, the first with six and the second with two setae; another four pairs of aggenital setae are arranged lateral to the genital valves (i.e. total aggenital setae = 16). Nine pairs of plumose genital setae, inserted close to inner margin of genital valves except for the laterally situated fifth pair. Seven pairs of plumose eugenital setae, most probably eupathidial in form, inserted on well sclerotized protuberances. Two pairs of genital papillae.

Podosoma (Figs 1B, 2, 6, 7). Coxal regions well developed, strongly sclerotized and ornamented; dorso-lateral surface rugose, especially on coxal regions I and II. Ornament on podosoma delicately punctate; between coxal regions IV with delicate pentagons. Contiguous coxal regions I and II clearly separated from contiguous coxal regions III and IV; coxal formula: 2-1-2-1. Sternal region well developed, much more delicately ornamented than coxal regions; sternal formula: 2-0-2-2. Sternal and coxal setae plumose.

Legs (Figs 6, 7). Legs shorter than idiosoma, leg I 348 long, Tr-Ts 30-110-50-58-100 long, leg II 265 (30-75-40-50-70 long), leg III 275 (30-85-40-50-70 long), leg IV 325 (30-100-50-65-80 long). Chaetotaxy and solenidiotaxy (in parentheses) for legs I to IV: Tr 1-1-1-1, F 9-7-5-7, G 5(1+f)-5(1+f)-5(1)-4(1), Tb 6(2)-6(2)-6(1)-6(1), Ts 23(2+1+f)-16(3+1)-15-15. Solenidia inserted dorsally, smooth, without striae. Rhagidial organ I with two banana-shaped solenidia (10 long each) in tandem in confluent depressions (Figs 6A, 7A). Distal depression below proximal depression, shorter than solenidion. Laterally, at level of proximal solenidion, one T-shaped solenidion (6 long) inserted in pit which is considerably larger than solenidion. Small stellate famulus positioned more proximally, completely distant from rhagidial organ I. Rhagidial organ II with three thin, baculiform solenidia (11, 10 and 9 long, respectively), in tandem in common depression; proximal

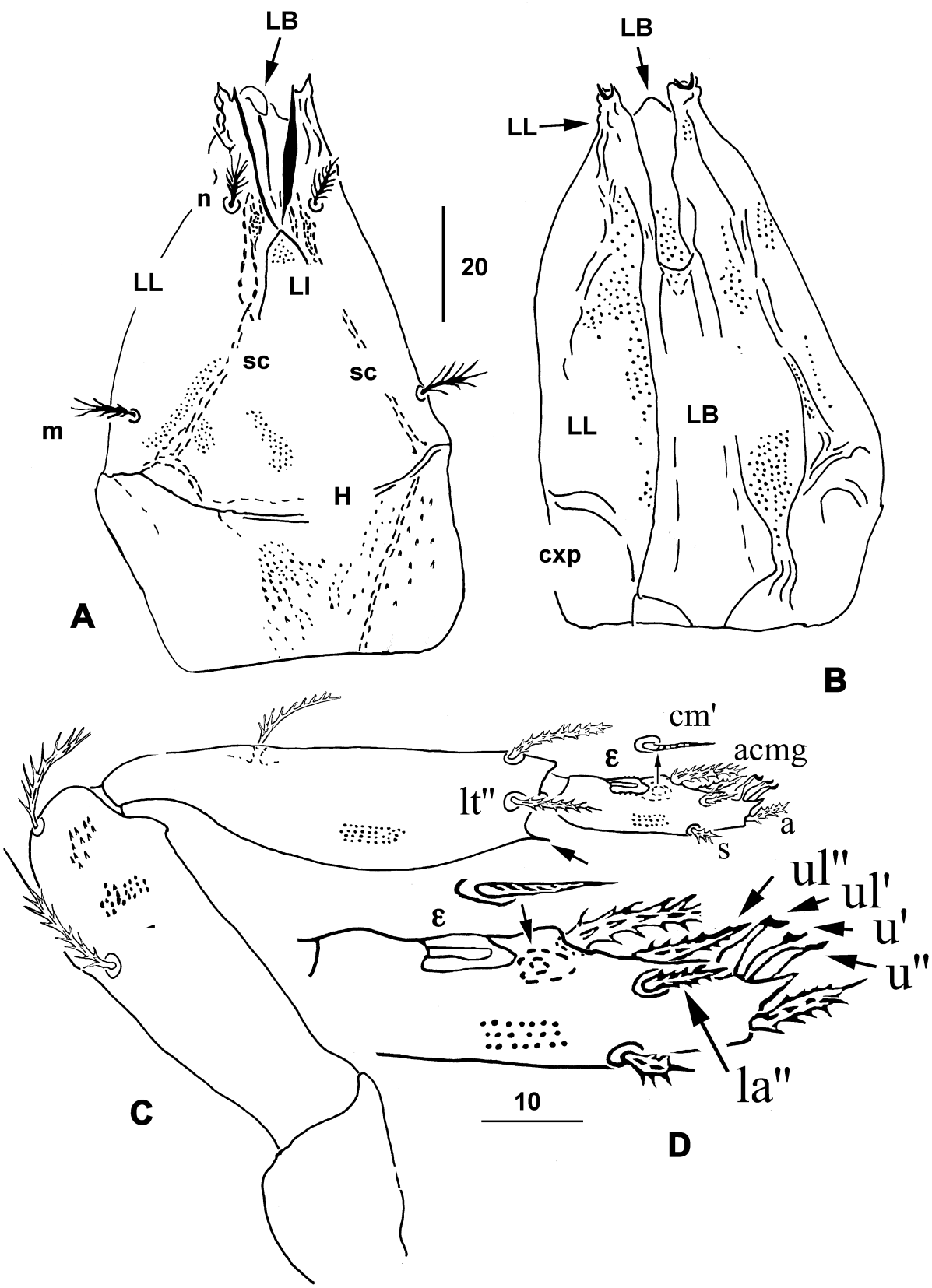

FIGURE 4. *Penthalodes polonicus* **n. sp.** (A) Subcapitulum, ventral view; (B) Subcapitulum, dorsal view; LB-labrum, LL-lateral lips, LI-labium, H-hypostome, sc-internal sclerites, n,m-subcapitular setae, cxp-coxal region of pedipalp. (C) Pedipalp, lateral view; (D) Pedipalpal tarsus in detail, lateral view.

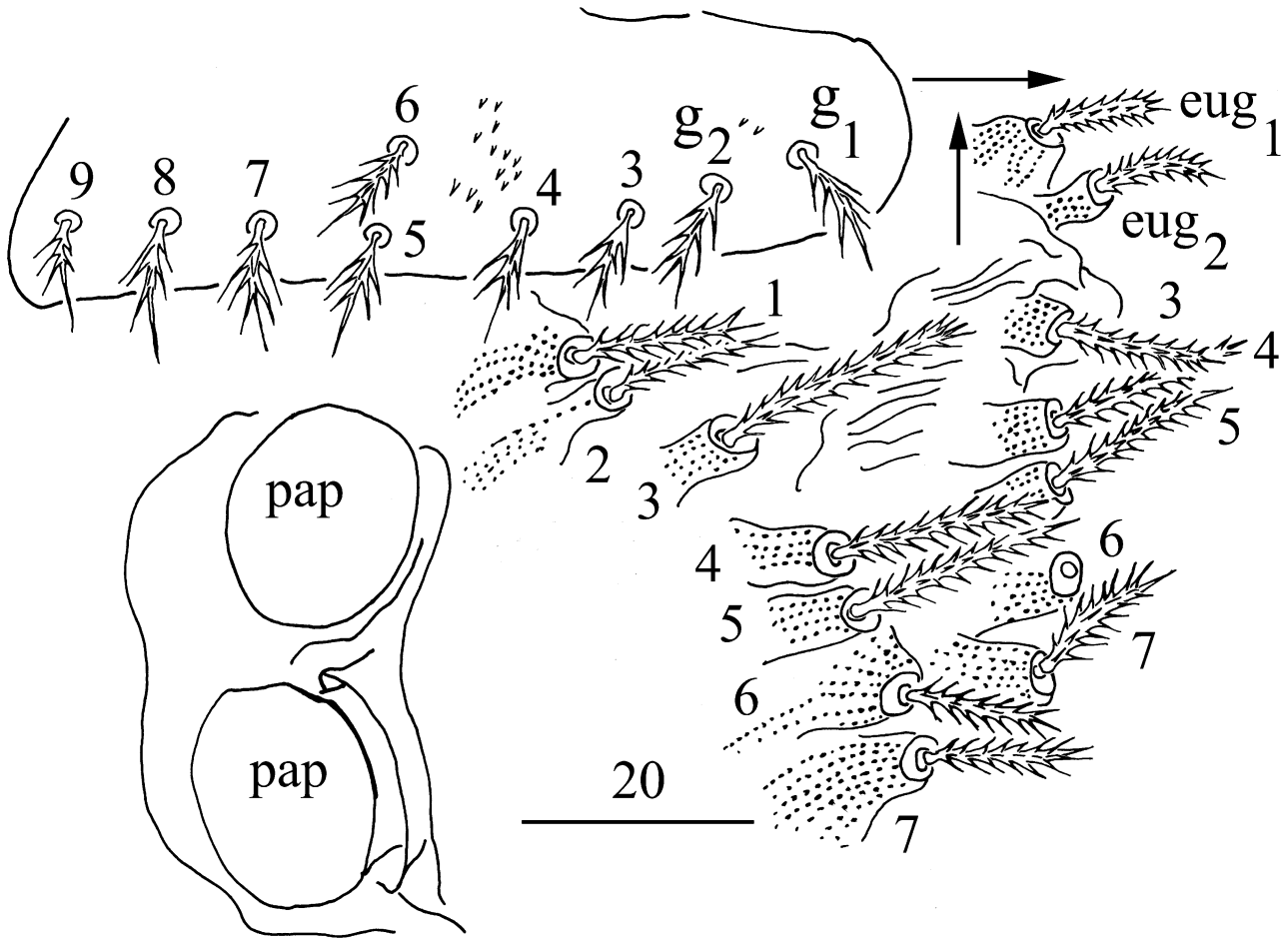

FIGURE 5. *Penthalodes polonicus* **n. sp.** Genital region. Genital valve with nine genital setae, g_1-g_9; seven pairs of eugenital setae, eug_1-eug_7; two pairs of genital papillae, pap_{1-2}.

solenidion the thickest; solenidia adjacent and overlapping one another because distal part of depression is positioned below proximal part (like cascade) (Figs 6B, 7B). Spine-like tiny solenidion (or famulus; 2 long) in small pit lateral to proximal solenidion. Tibia I with two dorsodistal solenidia, proximal solenidion (6 long) erect and baculiform, distal solenidion (8 long) banana-shaped, recumbent in depression; distal solenidion thickest; distance between solenidia 9. Tibia II with two dorsodistal solenidia; proximal solenidion (5 long), rod-like, distal solenidion (10 long) thick, banana-shaped, in depression; distance between solenidia 6. Tibia III and IV each with one erect, baculiform dorsoproximal solenidion (6 and 7 long, respectively). Genua I–IV each distally with large (especially large on G I, II and IV) banana-shaped solenidion (13, 13, 9 and 13 long, respectively); genu I and II each with tiny spiniform famulus (4 and 3 long, respectively; in own pore) located near distal margin of article; famulus on genu I with one lateral spine (bifurcate). Three pairs of setae expanded distally near apotele I-IV each. All leg setae shorter than leg article, plumose with long distal outgrowths (spicule), especially long on femur II setae. Ventral tarsal setae angled basally, i.e. foot-shaped. Leg integument strongly sclerotized with ornamentation composed of tiny spines and minute tubercles. Apotele I–IV each with ambulacrum composed of two claws and pad-like, setuled empodium. Ambulacrum of leg IV the largest.

Material examined. Female holotype (KJJ724-1), Zakopane. Tatrzański Park Narodowy (The Tatra Mountains National Park). Dolina Chochołowska (Chochołowska Valley). Stone under the peaks of "Olejarnia" in Niżna Brama Chochołowska; mosses, grass and soil. 20.09.1979. Leg. J. Rafalski. Three females, same data as holotype. Further material examined: two females (one paratype KJJ797-2), Zakopane. The Tatra Mountains National Park. "Wąwóz Kraków" (Krakow Ravine); mosses, grass, soil and detritus from stone cracks and cavities (limestone). 10.10.1983. Leg. Z. Olszanowski.

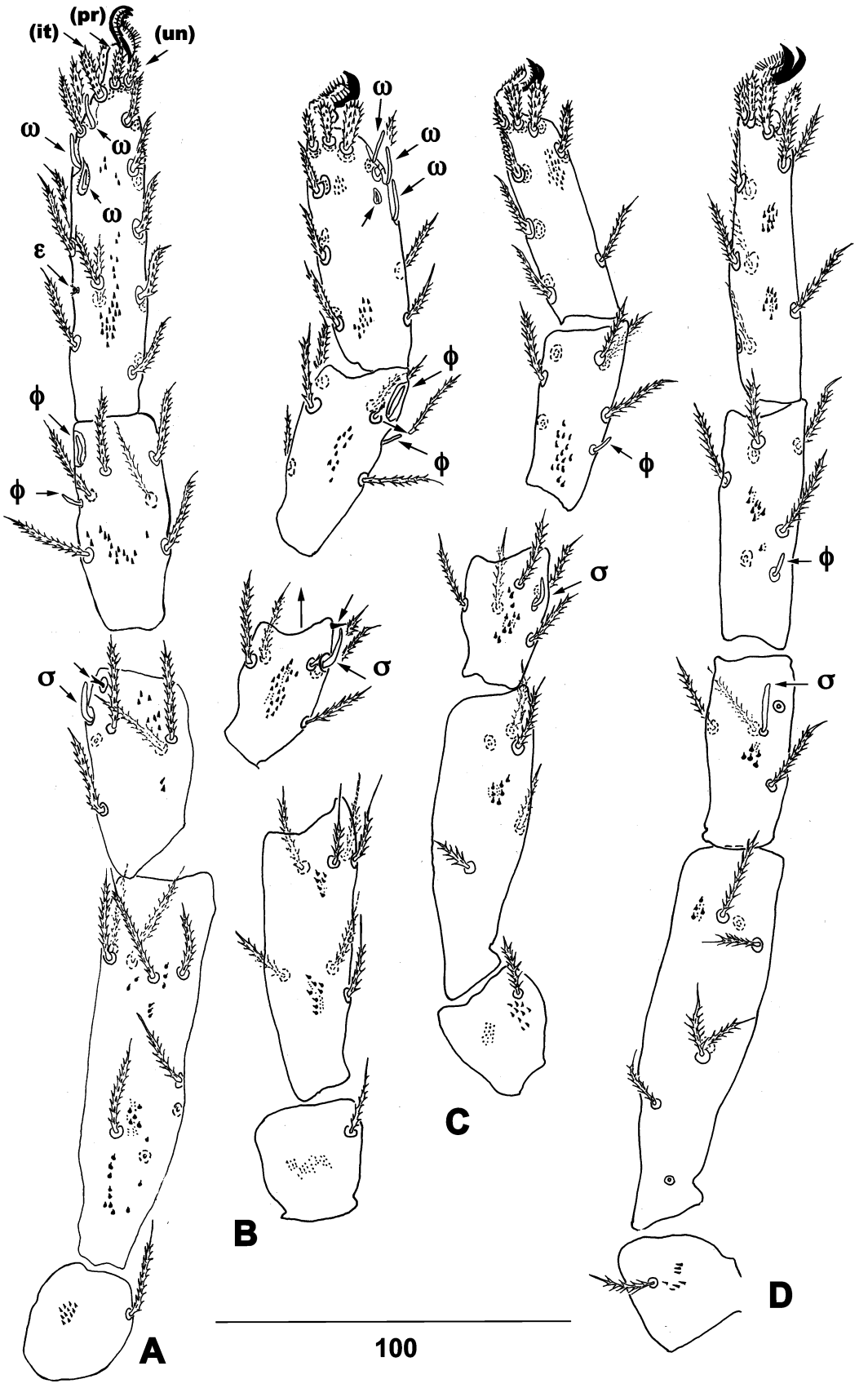

FIGURE 6. *Penthalodes polonicus* **n. sp.** (A) Leg I, lateral view. (B) Leg II, lateral view. (C) Leg III, lateral view. (D) Leg IV, tarsus and tibia-lateral view, femur and genu-dorsal view. Solenidia and famuli arrowed.

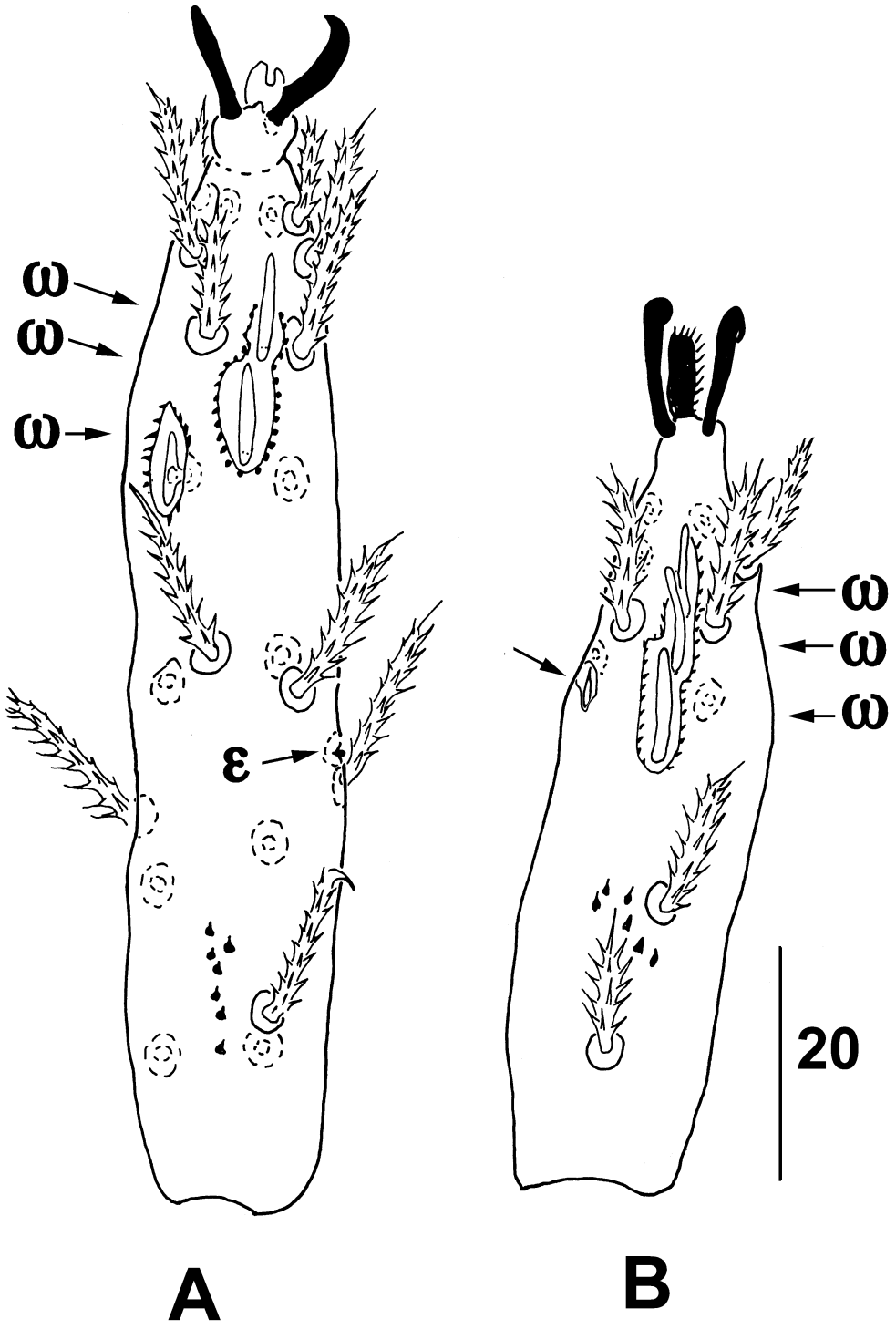

FIGURE 7. *Penthalodes polonicus* **n. sp.** (A) Tarsus I, dorsal view. (B) Tarsus II, dorsal view. Solenidia and famuli arrowed.

The material is deposited in the author's collection. In future, specimens will be transferred to the Acarological Collection of the Faculty of Biology, Adam Mickiewicz University, Poznań.

Etymology. The species name refers to the Polish part of the Tatra Mountains.

Differential diagnosis. This new species, although also European, differs from *P. ovalis* sensu Kaluz in the following combination of characteristics: (1) setae *ro* adjacent, i.e., inserted close to each other; (2) dorsal idiosomal setae tridactylate (except setae *ro* and *bo*); (3) epirostrum with weakly developed semi-round lateral

lobes; (4) epirostral ornamentation composed of irregular tubercles, not pentagons or reticular pattern; (5) solenidia in rhagidial organ I banana-shaped, in tandem in confluent depressions; not lanceolate; (6) all solenidia in the rhagidial organ II in tandem, slightly overlapping each other, thin and baculiform, none lanceolate; (7) lateral solenidion on tarsus I T-shaped, not spiniform; (8) pedipalpal tarsus elongated, linear in profile; (9) stellate famulus on tarsus I well removed from rhagidial organ I; (10) number of aggenital setae 16, not 23; in pregenital region, eight setae in two alignments (six and two, respectively), not 13 (five and eight, respectively); (11) seven pairs of eugenital setae.

In *P. ovalis* sensu Kaluz (2000), the solenidia on tarsi I and II are arranged in a specific way. Rhagidial organ I has two lanceolate solenidia arranged linearly in separate depressions, with a third spiniform solenidion placed laterally in a pit. Rhagidial organ II has a lanceolate proximal solenidion placed separately from two parallel distal solenidia in a common depression.

TABLE 2. Number of aggenital and genital setae in representatives of *Penthalodes.*

Species	Aggenital setae in pregenital region		Rest of aggenital setae	Total sum of aggenital setae	Genital setae
	first alignment	second alignment			
P. ovalis sensu Kaluz 2000 (Fig.2)	5	8	10	23	9+9
P. alaskaensis (Strandtmann 1971)	5	4	8 or 9	17 or 18	7+7
P.ovalis sensu Baker 1990	2	4	6	12	10+10
P. carinatus Shiba 1978	4	4	8	16	8+8
P. turneri Baker 1946	?	?	?	16	9+9
P. boneti Baker 1946	4	6	8	18	9+9
P. polonicus **sp. n.** (present paper)	6	2	8	16	9+9
P. hawaiiensis (Strandtmann et Goff 1978)	?	?	?	?	8+8 or 9+9
P. ovalis sensu Thor and Willmann, 1941	?	?	?	?	6+6

Discussion

Morphological survey of hitherto described representatives of the *Penthalodes*. Eight species of *Penthalodes* are now identifiable. Four species, *P. alaskaensis* **sp. n.**, *P. boneti*, *P. oregonensis* and *P. turneri*, are known from North and Central America (Baker 1946; Strandmann 1971), two species, *P. ovalis* and *P. polonicus* **sp. n.** are from Europe (Kaluz 2000; present paper), *P. carinatus* is from Japan (Shiba 1978), and *P. hawaiiensis* **sp. n.** is from Hawaii (Strandmann & Goff 1978).

The descriptions by Baker (1946), Strandmann (1971) and Strandmann & Goff (1978) are all lacking detail to some degree, but allow their recognition as distinct species. Baker's (1946) description details the shape of epirostrum, an important feature for separating these species. Nevertheless, drawings of rhagidial organ I and II and detail of other leg solenidia are lacking. Some data, now considered important in descriptions, are also missing from Strandmann (1971) and Strandmann & Goff (1978).

Shiba's (1978) description of *P. carinatus* is also brief, but is supported by drawings where, among others, the shape and the arrangement of solenidia on the tarsi and tibiae of legs I and II, as well as the shape of the epirostrum, distinguish this species from all others. However, Shiba (1978) thought the main character distinguishing it from similar species (*P. ovalis* and *P. boneti*) was the presence of eight pairs of genital setae. The redescription of *P. ovalis* by Kaluz (2000) presents good drawings for his putative *P. ovalis* specimens collected in Slovakia and Turkey.

Thor and Willmann (1941) promoted the use of the name *P. ovalis*, and the genus *Penthalodes*, by presenting a list of diagnostic characters for the genus: (1) epirostrum present; (2) reticulate ornament of the body composed of tetragons, pentagons or hexagons; (3) furrows in the form of the letter V on dorsum; (4) no epivertex (i.e. naso); instead of it, an eye-like organ with a pair of rudimentary hairs; (5) legs shorter than the body; and (6) setae of the body very small, plumose or branched. Due to Thor and Wilmann's (1941) work, most ecological works and check-lists use the name *P. ovalis* when they probably mean *Penthalodes* sp., because many do not make proper reference to the species-level characteristics.

The following morphological review allows for a new understanding of the characteristic features of adults of the genus *Penthalodes*, comparisons to other representatives of the Eupodoidea, and the new diagnoses and species already presented in this work.

Idiosoma. The idiosoma has characteristic shape; angular in profile, while being slightly narrowed posteriorly in dorsal view. Its anterior and posterior part is steep (Fig. 2). When viewed in lactic acid, it can be flattened laterally. Other authors describe it as plump, ovoid or almost globose. On the dorsum, there are characteristic furrows arranged like the letter "V" or "Y", depending on slide preparation.

Epirostrum. This structure resembles a small roof over the gnathosoma. The epirostrum is positioned well below the naso and is either trilobed or monolobed (Table 3). The central lobe is always obviously the largest. The epirostrum of *Penthalodes* sp. presented by Baker (1987) is most similar to *P. turneri*. Ornamentation on the epirostrum is usually reticulate in the basal part, and linear or punctate in the apical part, but does vary in some species. The profile of the epirostrum can differ, e.g. the dorsal line can be sloping from the base, as in *P. polonicus*, or can initially form a small platform (like in other representatives of the genus collected in Poland, Fig. 3E). The epirostrum does not occur in the larva and tritonymph (Jesionowska 1996; Strandtmann 1971).

TABLE 3. Form of the epirostrum in identifiable species of *Penthalodes; P. ovalis* is sensu Kaluz (2000).

Penthalodes	Lobes	Central lobe	Lateral lobes	Ornamentation
ovalis	3	Triangular	lingulate, directed obliquely	Wholly reticulate
alaskaensis	3	Pentagonal; broad base, short triangular tip	sharp apices directed antiaxially	Wholly reticulate
hawaiiensis	3	Triangular	slightly pointed, weakly separated from central lobe	Wholly reticulate
polonicus	3	Triangular	broadly rounded, weakly separated	Wholly punctuate with large and minute costulae
carinatus	1	Triangular; edges slightly plicate		Wholly reticulate
turneri	1	Triangular with rounded apex		Basally reticulate, apically striate
boneti	1	Rectangular or trapezoidal transformed medially into ligulate process, cusps slightly pointed		Basally reticulate, apically striate
oregonensis	1	Large, undivided, lobed, with broadly rounded apical part		Basally punctuate, distally with tiny hairs

Naso. The naso of *Penthalodes* is unique. It is spherical, smooth and completely disconnected from the epirostrum below. Only the anterior hemisphere of the naso is visible in dorsal view, while the other hemisphere is hidden in a cavity of the prodorsum wall. Strandtmann and Goff (1978) observed that the naso is submerged in the anterior part of idiosoma. A detailed description of the appearance of the naso is presented by Haupt and Coineau (2002), and its scanning electron micrograph is given by Baker (1990). The naso bears a pair of minute, nude, unbranched setae *ro*. Thor and Willmann (1941) considered the naso absent, but instead a an eye-like structure (organ) with a pair of rudimentary setae.

Idiosomal setae, except setae of the genital region and podosoma (Table 1). The number and the arrangement of idiosomal setae are characteristic for *Penthalodes*. They lack setae d_1 and *e.l.* (Strandtmann 1971), which are usually found in other Eupodoidea, making just 13 pairs of idiosomal setae, of which four

pairs fall on the prodorsum and nine pairs on the opisthosoma. Because the idiosoma is angular (geometric solid body), some setae are located on the steep walls of its anterior and posterior parts (Fig. 2). Therefore, it is difficult to be confident about setal names of the dorsum and the venter because they can optically change their location after flattening of the idiosoma. For example, setae c_2 may be placed slightly anterior to c_1, giving the illusion that they are prodorsal setae.

Strandtmann (1971) and Baker (1987) considered *Penthalodes* with four pairs of prodorsal and nine pairs of opisthosomal setae, contrary to Kaluz (2000) who proposed an unusual arrangement of five pairs of prodorsal and eight pairs of opisthosomal setae. The prodorsal setae are thought to be *iv*, ev_1, ev_2, *T* and *sc*. The extra prodorsal setae are obtained by considering the opisthosomal setae c_2 as the scapular setae *sc*. Five pairs of prodorsal setae are atypical for Eupodoidea, which have just four pairs of fundamental prodorsal setae. Baker (1987) distinguishes nine pairs of opisthosomal setae with total lack of setae *h*, whereas Kaluz presents only one pair of these setae (instead of two pairs like in other Eupodoidea). They both recognize two pairs of setae *f*, i.e. f_1 and f_2, and setae *ps*, –according to Kaluz- two pairs of setae *ps*, and -according to Baker- three pairs of these setae.

Here, I follow Strandmann (1971) by considering *Penthalodes* to have four prodorsal, and nine opisthosomal pairs of setae. In my opinion there are two pairs of setae *c*, c_1 and c_2, and only one pair of setae on segment from D to AN each, particularly only one pair of setae *f* and *h* (differently than Baker and Kaluz). Three pairs of setae *ps* (ps_1, ps_2, ps_3 according to Baker), I recognize as *ps*, *ad*, and *an*, respectively (Table 1). With only one pair of setae accompanying the anal cleft (*an*), not three or two.

Setae c_1 and *d* are positioned between furrows "V" and lyrifissures *ia* externally. Setal pair *e* lies laterally in relation to the furrows. Setae *f* are aligned with lyrifissures *ip*, and are lateral in relation to the "V" furrows. Setae *h* form a separate row posterior to setae *f* and situated more laterally than the other setae because the opisthosoma changes into steep wall at this position. One pair each of setae *ps*, *ad* and *an* lie at this posterior wall of the opisthosoma one under another. Only setae *an* are placed in close vicinity to the anal cleft (see also in larva, Jesionowska 1996). This idiosomal chaetotaxy is also characteristic of *Protopenthalodes* and *Hawaiieupodes* (Jesionowska 1989, 2008).

On the scanning electron micrograph published by Baker (Fig.19d in 1990), the arrangement of setae on the posterior part of idiosoma is visible, illustrating three pairs of setae, ps_1, ps_2 and ps_3. Setae ps_1 are more removed from each other than setae ps_2, while setae ps_2 are more removed than setae ps_3. This arrangement is usually different in other Eupodoidea. Moreover, distances between rows of these setae are considerable and seem to be equal, although setae ps_1 are located at a slightly larger distance from setae ps_2 compared with the distance between setae ps_2 and ps_3. It is clearly visible that three pairs of setae are placed one under another because the opisthosoma forms a steep wall in this place. The very short anal cleft has anal valves and is located on a semispherical protuberance (also visible on the photo in Baker 1990). Earlier, Thor and Willmann (1941) observed that the anal opening is located terminally and on a protuberance. This suggests the existence of a tiny peranal segment, PE. Proximally, just in front of it, there is a pair of setae ps_3 according to Baker, but in my opinion it is a pair of setae *an*. When assuming that segments form rings (which is showed by location of setae *ps*, *ad* and *an*), it is difficult to imagine one large segment PS with three pairs of setae one under another with a simultaneous lack of segment H and setae *h*. The location of setae ps_1, ps_2 and ps_3, i.e. *ps*, *ad* and *an* respectively, shows in this case that most probably there are three separate segments, namely PS, AD and AN, each with one pair of setae, while the terminally located anus lies on the last segment, i.e. on PE (Table 1; Fig. 2).

The structure of idiosomal setae can differ, with prodorsal setae (except setae *ro* and *bo*) being usually much larger than opisthosomal setae (especially well visible on Fig. 1 in Kaluz 2000). Thor and Willmann (1941) observed that setae in *P. ovalis* are very small, plumose or branched. Setae in specimens described by Kaluz (2000) are branched with few outgrowths. Baker (1946), when comparing *P. boneti* with *P. ovatus* Koch (i.e. *P. ovalis*), found that the form of setae of the dorsum differs. In *P. boneti*, branches are short, while in *P. ovatus* they are less numerous and can be as long as the main stem. This feature approximates *P. ovatus* to the newly described species, i.e. *P. polonicus*, where setae are tridactyl, although prodorsal setae *xa* and *le* also

have short outgrowths at the base of the stem. On the other hand, in *P. turneri* Baker (1946) distinguishes setae on the dorsum as “semi-plumose”, with three to five lateral branches, while the anterior setae are “six-rayed”. This resembles the shape of setae on the dorsum of *P. ovalis* described by Kaluz (2000). In *Penthalodes* sp. presented by Baker (1987), the setae are short and not loosely feathered, with a long apical spine, while in *P. ovalis* they are "densely spinose terminating in long filament" (Baker 1990). In *P. oregonensis* and *P. carinatus*, the setae are pilose rather than weakly plumose. In *P. alaskaensis*, they are plumose, while those in *P. hawaiiensis* are loosely plumose, with a longer apical outgrowth and sometimes also with some slightly longer lateral outgrowth. Usually, the podosomal setae and those of the genital region and a pair of setae *an* differ from other idiosomal setae, being plumose-pilose, which is particularly well shown in *P. polonicus* and *P. ovalis* sensu Kaluz.

Lyrifissures. In all species of *Penthalodes*, lyrifissures are distinct and always present as four pairs (*ia*, *im*, *ip*, *ih*?). Lyrifissures *ia*, *im* and *ip* are lateral to furrows V, with *ia* situated slightly posterior to setae c_1, *im* slightly anterior to setae *e*, and *ip* at the same level as setae *f*. The last pair, *ih*, is positioned on the ventral side of opisthosoma anterior to setae *an*. The lyrifissures are slit-shaped with heavily sclerotized margins and arranged transversally.

Genital region (Table 2). The number of setae of the genital region in *Penthalodes* is variable. However, the arrangement of aggenital setae on the region between the coxal regions IV and the anterior margin of the genital valves (i.e. the pregenital region) is characteristic for *Penthalodes*, being composed of two alignments. The other setae are arranged in a line around the genital valves. The number of setae in each alignment varies. For example, in *P. ovalis* sensu Kaluz (Fig. 2 in 2000), the two alignments of aggenital setae in the pregenital region comprises five setae in the outer row, and eight setae in the inner row; the remaining five pairs of setae are arranged around the genital valves (23 setae in total). In *P. polonicus*, six setae form the outer row and two setae form the inner row; the remaining number of setae is four pairs (16 in total; Fig. 1B). Other examples are presented in table 2. For *P. ovalis* specimens presented by Baker (1987), as well as specimens of *P. hawaiiensis* and *P. oregonensis*, there is no information on the aggenital region. The number of aggenital setae in *Penthalodes* representatives ranges from 12 to 23 setae and may fluctuate, in particular in the pregenital region.

The genital setae are inserted on strongly sclerotized genital valves, arranged linearly, close to the inner margin, usually with one pair situated more laterally. The number of genital setae varies from 6 to 10 pairs between species (Table 2). In *P. ovalis* sensu Baker (1990) the number of genital setae can be inferred from drawing only.

The number of eugenital setae has earlier been mentioned only by Strandtmann (1978) and Kaluz (2000) as six pairs in *P. ovalis* sensu Kaluz, contrary to *P. hawaiiensis* and *P. polonicus*, where there are seven pairs of setae.

Ornamentation of the idiosoma. The integument of *Penthalodes* species is moderately sclerotized with characteristic reticulate ornamentation formed by tiny, tubercular costulae creating pentagons and hexagons. The ornamentation is best discerned dorsally where costulae are large and distinct. On the other hand, the pattern is much more delicate, smaller on lateral and ventral parts, and can even disappear in the sternal region where it may be delicately punctate (particularly in the location of sejugal furrow). Around the genital valves, i.e. in the aggenital region, the delicate reticulate pattern sometimes disappears and tiny costulae form an irregular punctation, as in *P. polonicus*, whereas in other representatives, e.g. in *P. alaskaensis*, the reticulate ornamentation can be preserved. The coxal regions are strongly sclerotized, with a punctate or reticulate pattern, or a combination of punctate and reticulate ornamentation. In *P. polonicus*, there are sigillae visible between the coxal regions II and III, indicating the region of the sejugal furrow.

The lateral margins of the pentagons are formed by tubercular costulae which can be tear-shaped (more or less elongated), like in *P. polonicus* (Fig. 1), or have a broad basis terminating in a hook-like process, like in some *P. ovalis* (Baker 1990), or resemble a pyramid (Kaluz 2000). The surface area of the pentagons can be covered by tiny costulae in the form of dots forming parallel lines, like in *P. polonicus* and *P. ovalis* sensu Baker (1990), or can be visibly lined with single tiny costulae, like in *P. carinatus*, or smooth, like in *P. ovalis* sensu Kaluz. *Penthalodes hawaiiensis* has an ornamentation composed mainly of hexagons, with single

spines arranged rather irregularly within their areas. In some representatives of *Penthalodes* there are sometimes single, additional, large tubercular costulae on the pentagon surface. This may occur in all species.

In *P. ovalis* sensu Kaluz, the polygonal reticulate ornament occurs on the whole surface of the idiosoma, except the sternal region, and in some specimens, this polygonal pattern on the dorsum can be disturbed. In *P. boneti* the pattern is similar: a reticulate pattern between the coxal regions, except the sternal region where it becomes tuberculate (punctate). According to Baker (1946), it is similar to the ornamentation of *P. ovatus* (i.e. *P. ovalis*). In *P. carinatus*, the reticulate pattern of the whole idiosoma is composed of pentagons and hexagons. In *P. turneri* and *P. oregonensis*, it is composed of hexagons on the whole idiosoma (Baker 1946). In *P. alaskaensis*, the reticulate pattern occurs on the whole idiosoma but clear, regular pentagons and hexagons are most distinct on the dorsum and the ornament on the sternal region is reticulato-punctate (Strandtmann 1971). It is similar in *P. polonicus*.

TABLE 4. Solenidia of the rhagidial organ on tarsi I and II in representatives of *Penthalodes*.

Penthalodes	Solenidia of rhagidial organ I		
	Number	Shape	Arrangement
alaskaensis	2	baculiform; equal in size	recumbent in tandem; in confluent depressions
boneti	2+1	rod-like	in line; third laterally
carinatus	2	slightly T-shaped	in tandem, in separate depressions
hawaiiensis	2+1	baculiform; third small and spatulate	recumbent in tandem; in confluent depressions; third laterally
oregonensis	2+1	rod-like	in line; third laterally
ovalis sensu Kaluz (2000)	2+1	lanceolate sharply tipped; third small rod-like	in line in separate depressions; third laterally
ovalis sensu Baker (1990)	2+1	baculiform, equal in size; third tiny papillate	semi-erect in line in short common depression; third laterally
polonicus	2+1	banana-shaped; third small T-shaped	recumbent, in tandem in confluent depressions
turneri	2+1	rod-like	in line; third laterally

continued.

Penthalodes	Solenidia of rhagidial organ II		
	Number	Shape	Arrangement
alaskaensis	3	baculiform; two proximal equal in size; third distal longest	recumbent in tandem; in confluent depressions
boneti	3	rod-like	in line
carinatus	3	slightly T-shaped	in separate depressions; two distal parallel
hawaiiensis	3+1(f?)	baculiform, unequal size: proximal longest and thickest; distal smallest and thinnest; fourth tiny spine-like posteriorly	staggered in confluent depressions
oregonensis	3	rod-like	in line
ovalis sensu Kaluz (2000)	3	proximal lanceolate sharply tipped; two distal baculiform	proximal in own depression separately; two distal parallel in common depression
ovalis sensu Baker (1990)	?	?	?
polonicus	3+1(f?)	thin baculiform, almost equal, proximal thickest; fourth tiny spine-like laterally	in tandem in common depression, overlapping one another
turneri	3	rod-like	in line

Rhagidial organs, solenidia and leg setae (Tables 4, 5). The rhagidial organ on tarsus I consists of two dorsal solenidia and a small lateral solenidion. The rhagidial organ on tarsus II consists of three dorsal solenidia and a small, rod-like solenidion (or famulus?) lying laterally in a separate pit. Species differences

result from solenidia shape, the manner of their arrangement as well as whether they lie in common or separate depressions. It seems that in species of *Penthalodes* there are no famuli typical of other Eupodoidea. Most probably they are replaced by a tiny solenidion. In some species, however, there is a small, stellate famulus on tarsus I. This famulus is placed a small distance from the rhagidial organ in *P. carinatus* or laterally and far behind it in *P. polonicus*. Strandmann (1971) also reported a famulus in *P. alaskaensis*, accompanying the rhagidial organ. However, after repeated verification, he considered it is missing, particularly in specimens from Hawaii (Strandtmann & Goff 1978). Famuli are not known in other species.

TABLE 5. Solenidia on tibiae and genua in representatives of *Penthalodes*. No data available for *P. boneti*, *P. oregonensis* and *P. turneri*. Abbreviations: DD = dorsodistal; DM = dorsomedial; DP = dorsoproximal.

Penthalodes	Tibia I	Tibia II	Tibia III	Tibia IV
alaskaensis	2 DD in line: one in pit and longer one piliform	2 DD in line: one in pit and longer one piliform	1 DM, erect	1 DM, erect
carinatus	2 DD in line: one thicker baculiform (T) in pit and much longer one thin piliform	2 DD in line: one thicker baculiform (T) in pit and slightly longer one thin piliform	1 DM, erect	1 DM, erect
hawaiiensis	2 DD in line: one thicker rod-like in pit and longer one thin piliform	2 DD in line: one thicker rod-like in pit and longer one thin piliform	1 slender erect	1 slender erect
ovalis sensu Kaluz (2000)	2 DD in line: one longer rod-like in pit and one thicker sharply-tipped spiniform	2 DD in line: one slightly thicker and longer rod-like in pit and one spiniform	DP short baculiform	DP slightly longer than that on Tb III baculiform
ovalis sensu Baker (1990)	?	?	?	?
polonicus	2 DD in line: one thicker banana-shaped in pit and shorter one baculiform	2 DD in line: one longer thick banana-shaped in pit and one rod-like	1 DP erect baculiform	1 DP erect baculiform

continued.

Penthalodes	Genu I	Genu II	Genu III	Genu IV
alaskaensis	1 DD, erect; plus 1 tiny famulus at dorsal anterior margin	1 DD, erect; plus 1 tiny famulus at dorsal anterior margin	1 DD, erect piliform	1 DD, erect piliform
carinatus	1 DM, erect	1 DM, erect	1 DM, erect	1 DM, erect
hawaiiensis	1 DM, erect piliform; plus 1 tiny famulus at dorsal anterior margin	1 DD, erect piliform; plus 1 tiny famulus at dorsal anterior margin	1 slender erect	1 slender erect
ovalis sensu Kaluz (2000)	1 DM, erect short spiniform	1 DM, erect short spiniform	1 DM erect baculiform	1 DD erect baculiform
ovalis sensu Baker (1990)	?	?	distal papilla (Fig.13f)	?
polonicus	1 distal large banana-shaped; plus 1 tiny bifurcate famulus at dorsal anterior margin	1 distal large banana-shaped; plus 1 tiny spiniform famulus at dorsal anterior margin	1 distal banana-shaped	1 distal banana-shaped

The lateral solenidion on tarsus I is always very small and situated in a separate depression. In *P. ovalis* sensu Kaluz, it is rod-like (according to Kaluz, it is spiniform; see also Fig. 13c in Baker 1990) and is placed behind the rhagidial organ. In *P. polonicus*, on the other hand, it is relatively large, T-shaped and is situated at the level of the proximal solenidion. Baker (1946) mentions the lateral solenidion (as a sensory seta) of the rhagidial organ in all species described by him; it is rod-like as other solenidia. A similar situation occurs in *P. hawaiiensis*. In *P. carinatus*, Shiba did not observe the solenidion of that type.

The two solenidia of rhagidial organ I can be in tandem in confluent depressions, like in *P. alaskaensis* and *P. polonicus*, or in separate depressions, like in *P. carinatus* and *P. ovalis* sensu Kaluz. Solenidia are usually baculiform, except in *P. ovalis* sensu Kaluz, where they are lanceolate and sharply tipped; in *P. carinatus* they resemble the letter "T"; and in *P. polonicus* a banana. In *P. polonicus*, the distal solenidion protrudes from the short depression; it is also characteristic that the distal depression is below the proximal one. The solenidia in *P. ovalis* sensu Baker (1990) are semi-erect because the depression, in which they are inserted, is short.

The three solenidia of rhagidial organ II can be arranged one behind another in confluent depressions, like in *P. alaskaensis, P. boneti, P. hawaiiensis* and *P. polonicus*. Otherwise, in *P. ovalis* sensu Kaluz two distal solenidia are parallel and situated in a common depression. *P. carinatus* is similar, but has separate depressions. In *P. hawaiiensis*, the bases of the solenidia do not lie in one line but are staggered in tandem. In *P. polonicus*, the solenidia are in one line but overlap each other because the depression is short resembling a cascade. In *P. ovalis* sensu Kaluz, two distal solenidia are baculiform, while the proximal solenidion is lanceolate. In *P. carinatus*, the solenidia slightly resembles the letter "T". In *P. hawaiiensis*, they are baculiform and of different length and thickness; the proximal solenidion is the thickest and longest, while the distal one is the thinnest and shortest. In *P. polonicus*, differences between solenidia are slightly less visible; and laterally to rhagidial organ II lies a small, spiniform solenidion or famulus (?) in a pit, like in *P. hawaiiensis*. This structure resembles a solenidion because it is hollow (transparent) proximally, while being solid (non-transparent) distally like a famulus. In other species, this has not been observed.

The occurrence of solenidia on all tibiae and genua, plus single famuli on genu I and II near the distal margin of the article, is characteristic for *Penthalodes*. Famuli are not recorded in other descriptions, although Strandtmann (1971) observed tiny sensory setae and Baker (1990) mentioned a characteristic papilla on genu III. On tibiae I and II, the distal solenidion is situated in a depression, while the proximal solenidion is erect. Particularly large disproportions in the size of solenidia on tibia II occur in *P. polonicus*, where the distal solenidion is very thick, and at least by half as long as the tiny, rod-like proximal solenidion. In *P. carinatus*, the proximal solenidia are erect, sharp-pointed and clearly longer than the distal solenidia, which are thicker, rather T-shaped, and pointed distally. *P. hawaiiensis* is similar, where the proximal solenidia are thin and longer than the rod-like, slightly thicker distal solenidia. In *P. ovalis* sensu Kaluz, on tibia I the distal solenidion is rod-like and slightly longer and thinner then the proximal solenidion; on tibia II, the proximal solenidion is short and piliform, while the distal solenidion is rod-like and slightly thicker and longer than the proximal solenidion. The bases of distal solenidia lie in a deep pit so that only the distal part is visible from the pit aperture. Solenidia on genua I and II in this species are very short and spiniform, contrary to *P. polonicus* where they are large, thick and banana-shaped. Solenidia on genua III and IV in *P. ovalis* sensu Kaluz are of similar length and thickness, contrary to *P. polonicus* where the solenidion on genu IV is thicker and longer than that on genu III. In both species, solenidia on tibiae III and IV are of subequal length and thickness. For other species, there are no detailed descriptions or drawings.

Leg setae are characteristic for *Penthalodes*. In *P. polonicus*, they are rather plumose and have a short shaft with triangular outgrowths, with the apical outgrowth being clearly the longest. At the base of each apotele are three pairs of thick setae, expanded distally, which are distinct in *P. polonicus* and *P. hawaiiensis*. In other species there is no information, although Strandtmann (1971) noted the occurrence of four pairs of apical setae on all tarsi (i.e. those lying close the apotele) as well as the occurrence of a single dorsal seta in the proximal part of the article as a characteristic feature of *Penthalodes*.

Aspidosoma. The aspidosoma is not separated from the rest of the body because the transverse "das" furrow is absent. In other eupodoids it usually separates the prodorsum from the opisthodorsum. The usually characteristic prodorsal plate of eupodoids is also absent. The ornamentation of the prodorsum is the same as the opisthodorsum. On the sides of prodorsum, more or less behind setae *xa*, the V-shaped furrows begin. All *Penthalodes* have a prodorsum with an anterior, steep wall of the aspidosoma, i.e. in fact of the idiosoma. Therefore, the naso lies frontally, more or less half-way up the anterior wall of the idiosoma. Setal pairs *le* and *xa* are also situated frontally. Setae *le* are well removed from setae *bo*, while setae *xa* lie laterally, slightly behind the line of setae *le*. Prodorsal setae *bo* lie as far back as between furrows "V", in deep bothridia, rather dorsally. In *P. polonicus*, they are filiform (sensu Jesionowska 2002) in their distal part, while the proximal

part is covered with tiny hairs. It is similar in *P. hawaiiensis* except they are weakly plumose in the distal part because they have more thickly placed outgrowths (pers. observations). The drawing from Strandtmann, however, seems to show they are filiform. In *P. ovalis* sensu Kaluz, they are spiculate distally. In *P. carinatus*, they are apically pilose, like in the species described by Baker (1946). In *P.* sp. presented by Baker (1987), setae *bo* are strikingly short and rather filiform on their whole length. Therefore, most probably, setae *bo* in representatives of the genus *Penthalodes* are weakly plumose in their distal part (or spiculate, or pilose).

Eyes. Lentiform eyes have been observed in most representatives of *Penthalodes*. On the photograph published by Baker (1990), fine striation of their surface is seen. The eyes are situated behind setae *xa*, laterally, more or less at the level of where furrows "V" start.

Gnathosoma. The lack of a cheliceral seta is most probably characteristic for *Penthalodes*. The shape of the profile of the pedipalpal tarsus differs in some species. The tarsus can be elongated (*P. alaskaensis*, *P. ovalis* and *P. polonicus*) or shorter, similar to an oval (*P. carinatus*). In *P. alaskaensis*, *P. carinatus*, *P. hawaiiensis*, *P. ovalis* and *P. polonicus* a small rod-like solenidion is recumbent in a depression. In *P. hawaiiensis* and *P. polonicus*, the tip of the three apical setae each on the pedipalpal tarsus is characteristic; they bear strongly sclerotized shuttles (carinas; Fig. 4CD). According to Kaluz (2000), two apical setae are solenidia, while Strandtmann (1971) and Baker (1946) stated only that they are nude. For other species, sufficient descriptions and drawings are lacking. On the subcapitulum, a pair of setae *n* (sbc_2) lies more or less at the level of the labium, while setae *m* (sbc_1) lies laterally, antiaxially, at the base of the lateral lips fused in that part of subcapitulum with the hypostome. In *P. hawaiiensis*, they are rather plumose, in *P. ovalis* sensu Kaluz pilose, while in *P. polonicus* they are weakly plumose with rather long lateral outgrowths. The hypostome, which forms ventral part of subcapitulum, is composed of two parts, a basal rectangular and a distal triangular part. Usually, the inner sclerite is visible that separates these parts (Fig. 4A; Fig. 5B in Strandtmann 1971).

Conclusions

Further detailed morphological studies on *Penthalodes* species, including those of original putative *locus typicus*, are necessary to elucidate true species diversity of this genus. Particularly *P. ovalis* sensu lato from different geographic areas is suspected to be a complex of different species, although I cannot yet rule out intraspecific variability. Features that should be the basis for species identification are the epirostrum shape and ornamentation, shape and arrangement of leg solenidia as well as shape of dorsum setae.

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