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# THE ISMARDIIDAE LEIGH-SHARPE (COPEPODA, HARPACTICOIDA *INCERTAE SEDIS*): ENIGMATIC AS EVER?

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ABSTRACT

Re-examination of the type material of *Ismardis spartacus* Leigh-Sharpe, 1936 (Copepoda, Harpacticoida), discovered in the gonad and mantle cavity of *Patella caerulea* L. (Mollusca), revealed that the species should be allocated to the genus *Harpacticus* Milne-Edwards, 1840, and not to the Thalestridae as previously suggested. The genus *Ismardis* and the family Ismardiidae are relegated to junior synonyms of *Harpacticus* and Harpacticidae, respectively. *Harpacticus spartacus*, new combination, is conspecific with the "schwächeren" form of the Mediterranean *H. nicaeensis* Claus, 1866. The taxonomic confusion surrounding *H. gracilis* Claus, 1866 is reviewed, and the species is regarded as unrecognizable, rendering all subsequent records unconfirmed, doubtful, or erroneous. At least some material previously identified with this species proved to be conspecific with *H. longiantennata* Apostolov and Petkovski, 1980 (Banyuls-sur-Mer) or based on an amalgamate of *H. obscurus* T. Scott, 1895, and *H. giesbrechti* Klie, 1927 (Norway). Several species formerly relegated to junior synonyms of *H. gracilis* are reinstated as *species inquirendae*: *H. elongatus* Boeck, 1865; *H. dentatus* Krichagin, 1873; and *H. fucicolus* T. Scott, 1912. The only European record of *H. pulvinatus* Brady, 1910, being otherwise endemic to the Southern Hemisphere, is based on a misidentification, being attributable to *H. nicaeensis*. Other records of the latter from outside the Ponto-Mediterranean basin are unverifiable and probably false, including the Angolese material of *H. nicaeensis*, which is regarded as *species inquirenda* in *Harpacticus*.

Symbiotic associations between harpacticoid copepods and molluscan hosts are rare and almost exclusively confined to the copepod family Tisbidae. Within the latter, all representatives of the Cholidyinae and two genera of the Tisbinae (*Octopinella* Avdeev, *Yunona* Avdeev) utilize benthopelagic and benthic deep-sea octopuses as hosts (Humes and Voight, 1997). Some species, such as *Avdeevia antarctica*, parasitic on the gills of the Antarctic cephalopod *Megaleledone senoi* Taki, 1961, can be considered as the most highly transformed harpacticoids known to date (Bresciani and Lützen, 1994). López-González *et al.* (2000) reinterpreted the life cycle of the Cholidyinae and suggested that there is a free-living naupliar phase followed by endoparasitic (copepodids) and ectoparasitic phases (adults).

Bivalves also serve as hosts for tisbid harpacticoids. Humes (1954) reported a new species, *Tisbe celata*, from the mantle cavity of *Mytilus edulis* L. in New Brunswick. His observations of copepodid stages on the gills indicated that *T. celata* is a genuine associate of the edible mussel rather than a free-swimming species accidentally introduced in the mantle cavity. A second, closely related species was recently discovered in the South American blue mussel *Mytilus edulis chilensis* Hupé, 1854, collected in Argentina (Huys, unpublished). The only association between marine gastropods and harpacticoid copepods was reported by Branch (1974) who found large numbers of *Scutellidium patellarum* Branch, 1974, associated with five species of *Patella* L. in South Africa. All developmental stages were associated with the limpets and appeared to be restricted to the pallial cavity.

In a paper dealing with new parasitic copepods from Naples, Leigh-Sharpe (1936) reported a new harpacticoid, *Ismardis spartacus*, from the gonad and mantle cavity of *Patella caerulea* L. He also introduced a new family Ismardiidae without any further discussion of its relationships and no justification for this course of action other than that he was unable to place *I. spartacus* in any of the existing harpacticoid families. Lang (1948) suspected that *I. spartacus* belonged to the Thalestridae but failed to make a firm recommendation for this assignment. He pointed out several deficiencies in Leigh-Sharpe's original description and consequently considered the Ismardiidae as unidentifiable, relegating the family as *incertae sedis* in the Harpacticoida.

In an attempt to resolve the last remaining enigma at family level within the Harpacticoida, we have re-examined the type material of *I. spartacus* deposited in The Natural History Museum. In this paper, we present evidence that Leigh-Sharpe's (1936) original description in reality was based on a representative of the family Harpacticidae, provide a redescription of *I. spartacus*, and discuss other harpacticid records in the Mediterranean Sea that are potentially attributable to this species.

## Materials and Methods

Both type specimens were restored from their original Euparal slide mounts by dissolving them in absolute acetone (after partly removing the coverslips) and subsequently clearing them in lactic acid. The adult male was dissected in lactic acid, and the dissected parts were mounted on slides in lactophenol mounting medium. Preparations were sealed with transparent nail varnish. All drawings have been prepared using a *camera lucida* on a Leitz DMR or a Zeiss Axioskop differential interference contrast microscope.

The descriptive terminology is adopted from Huys *et al.* (1996). Abbreviations used in the text are: ae, aesthetasc; exp, exopod; enp, endopod; P1–P6, first to sixth thoracopod; exp(enp)-1(2, 3) to denote the proximal (middle, distal) segment of a ramus. Type series is deposited in the collections of The Natural History Museum, London (NHM). Scale bars in figures are indicated in μm.

## Results

### Family Harpacticidae Dana, 1846
### Genus *Harpacticus* Milne-Edwards, 1840
### ***Harpacticus spartacus*** (Leigh-Sharpe, 1936), new combination

*Ismardis spartacus* Leigh-Sharpe, 1936.
*Harpacticus nicaeensis* Claus, 1866-"schwächeren Form."
*Harpacticus nicaeensis* Claus, 1866-"schwächeren Form" *sensu* Steuer (1937).

*Type Locality*.—Naples, Italy.

*Type Material*.—One adult male, dissected on 17 slides (NHM reg. no 1936.3.6.4), here designated as lectotype; paralectotype is a copepodid IV female in ethanol (NHM reg. no 1936.3.6.5). Originally labelled as *Ismardis spartacus*. Coll. M. Rothschild, 08 April 1934, from gonad and mantle cavity of *Patella caerulea*; det. H. Leigh-Sharpe.

*Redescription of Lectotype Male*.—Body length measured from tip of rostrum to posterior margin of caudal rami: 925 μm. Cephalosome and pedigerous somites with numerous integumental sensilla as figured (Fig. 1A). Rostrum (Fig. 1B) 1.4 times as long as maximum width, bell-shaped, with middorsal pore near proximal margin and 2 pairs of sensilla; anterior pair short, posterior pair long and delicate. Pedigerous somites without distinct hyaline frills or spinule rows, except for P5-bearing somite with 2 lateral spinule rows (Fig. 7C). All urosomites without middorsal spinules (Fig. 7B). Genital somite with 2 spinule rows laterally but none ventrally (Figs. 3D, 7A). First and second abdominal somites with oblique spinule row laterally and transverse spinule row ventrally (Figs. 3D, 7A). Third abdominal somite without spinular ornamentation but rows of tiny denticles present dorsally as on preceding somite (Fig. 7B). Anal somite with vestigial anal operculum, largely concealed under hyaline frill of penultimate somite (Fig. 7B); posterior margin with spinules laterally and ventrally as illustrated in Figs. 3A and 7A. Caudal rami (Fig. 7D) wider than long, with 7 setae; seta I small, surrounded by spinules; seta II located near seta III at outer distal corner; setae IV and V well developed, with predesigned fracture planes and fused at base; seta VI arising from small tubercular outgrowth at inner distal corner; seta VII tri-articulate at base; ventral posterior margin with large vent pore and numerous spinules as illustrated in Fig. 3D.

Antennule (Figs. 2A–C, 3A) 8-segmented, with geniculation between segments 6 and 7, and U-shaped sclerite around base of segment 1. Segment 1 large and swollen, with 3 spinular combs around anterior margin. Segment 5 represented by minute sclerite bearing 2 setae. Segment 6 with surface fold (possible representing original segmentation: Fig. 2A), several characteristically modified elements and series of overlapping pectinate ridges as figured in Figs. 2A and 3A; basally fused aesthetasc and seta arising from cylindrical pedestal; anterior surface with minutely serrate lamelliform outgrowth. Segment 7 with anterior concavity from which 2 small setae arise (Fig. 2A, B). Segment 8 small, irregularly shaped with transverse sutures but no functional articulations; ventral surface with 2 minute elements (Fig. 2C). Aesthetascs present on segments 3, 4, 6, and 8. Armature formula: 1-[1], 2-[1], 3-[11 + ae], 4-[7 + ae], 5-[2], 6-[6 + 8 modified + (1 + ae)], 7-[4], 8-[6 + 2 minute + acrothek]. Apical acrothek consisting of 2 long setae and aesthetasc.

Antenna (Fig. 3B, C) comprising coxa, allobasis, 2-segmented exopod and 1-segmented endopod. Coxa and allobasis without ornamentation. Abexopodal seta on allobasis bipinnate. Endopod with transverse row of large spinules

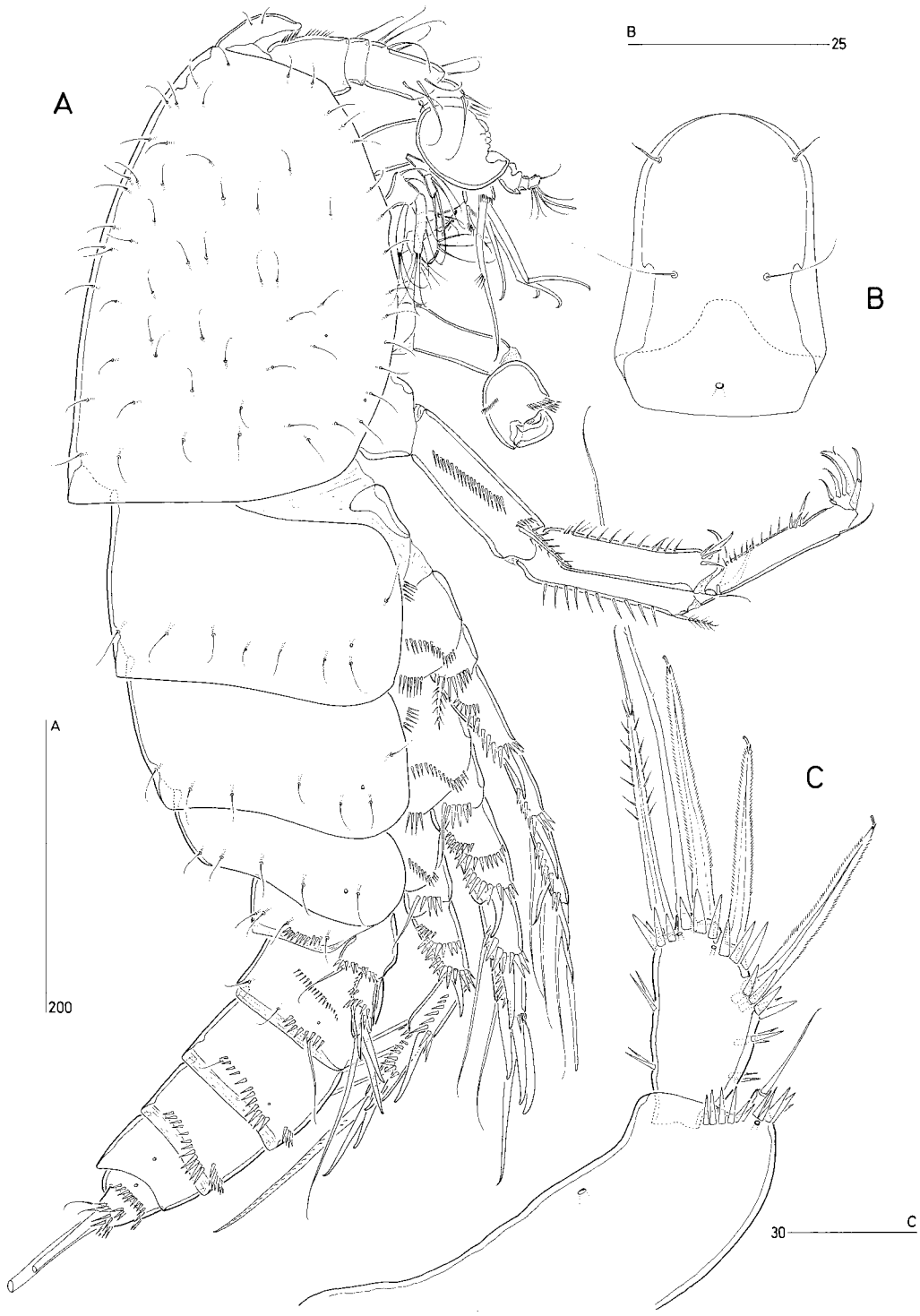


Fig. 1. *Harpacticus spartacus* (Leigh-Sharpe, 1936), new combination (♂). A, Habitus, lateral; B, Rostrum, dorsal; C, Right P5, anterior.

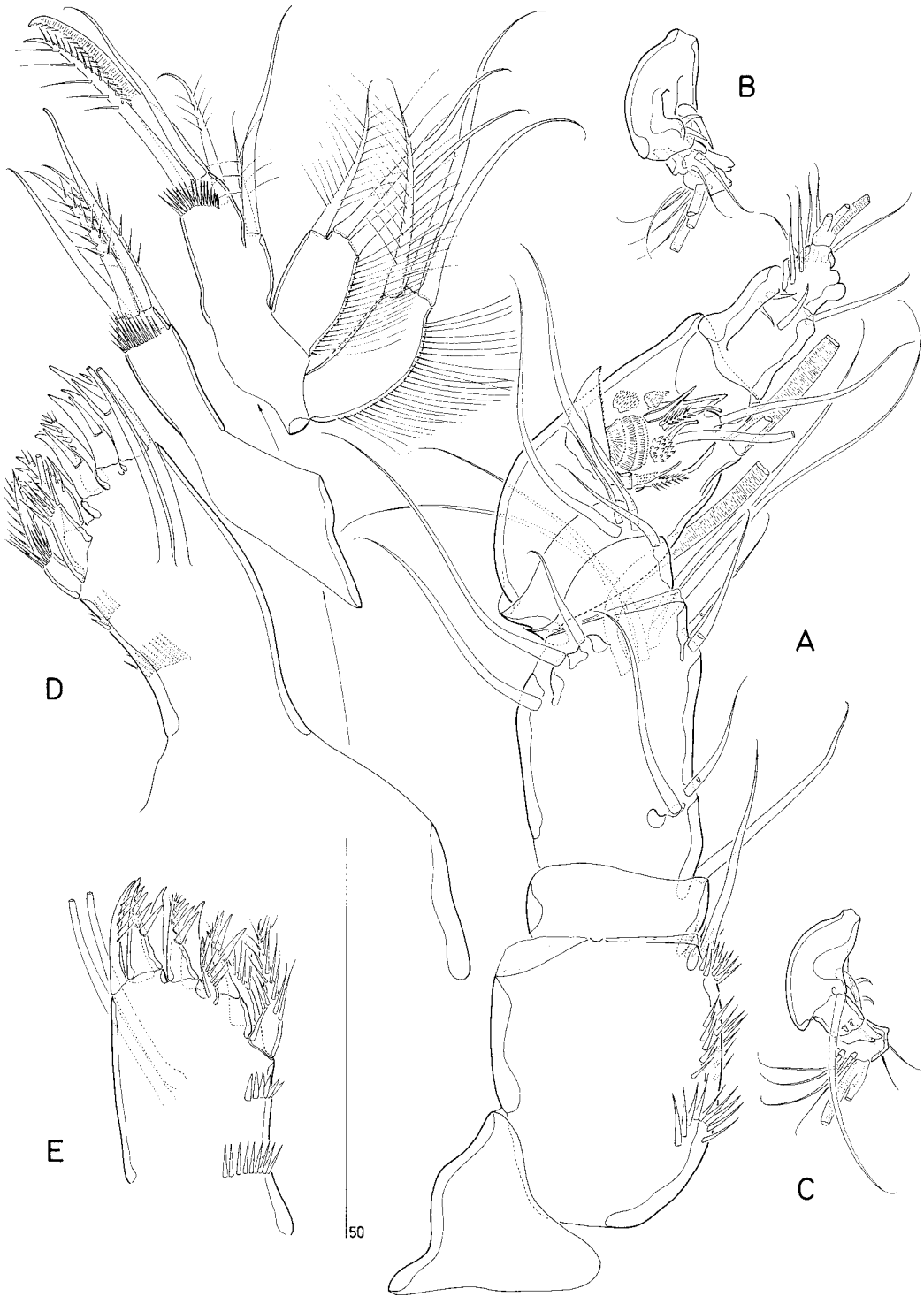


Fig. 2. *Harpacticus spartacus* (Leigh-Sharpe, 1936), new combination (♂). A, Antennule, dorsal (for complete setal counts of segments 4–6 see Fig. 3A); B, Antennulary segments 7–8, dorsal; C, Same, ventral; D, Maxillule, anterior [with syncoxa, coxa and palp diarticulated]; E, Maxillulary arthrite, posterior.

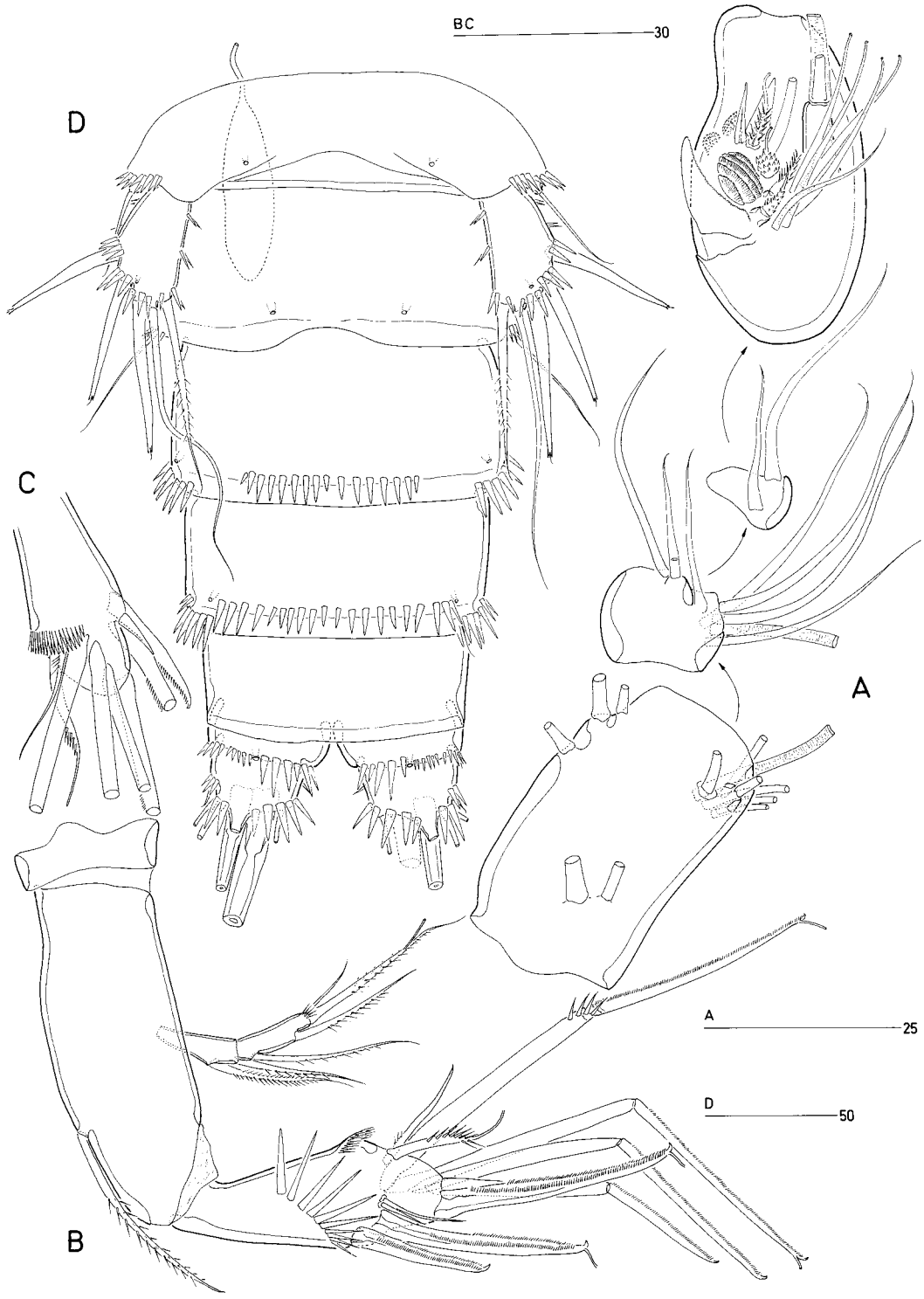


Fig. 3. *Harpacticus spartacus* (Leigh-Sharpe, 1936), new combination (♂). A, Antennulary segments 3–6, anterior; B, Antenna, inner; C, Distal portion of antennary endopod, outer; D, Urosome, ventral.

halfway up segment; lateral armature consisting of 2 small bare setae and 2 biserrate spines; apical armature comprising 4 geniculate setae (largest with spinules around geniculation), 1 biserrate spine and 2 sparsely pinnate setae near distal outer corner (surrounded at base by surface frill: Fig. 3C). Exopod with 1 bipinnate and 1 unipinnate seta on exp-1; exp-2 with 2 unipinnate setae laterally and 1 tiny bare seta plus 1 long bipinnate seta (with characteristic subapical tubular extension) apically.

Mandible (Fig. 4A, B) with robust gnathobase provided with series of multicuspidate teeth and strong, coarsely pinnate, dorsal seta. Palp comprising basis and 1-segmented rami. Basis with 4 setae (details not discernible because of damage). Endopod slightly longer than exopod; with 3 lateral setae; apical armature consisting of 10 setae, of which 7 are arranged in 2 basally fused clusters of 3 and 4, respectively. Exopod with 3 lateral setae (proximalmost arising near base of exopod) and 3 basally fused setae apically.

Maxillule (Fig. 2D, E) with elongate arthrite bearing 2 tube-setae on anterior surface, 2 spinular rows around inner margin and 10 ornamented spines around distal margin. Coxal endite with spinule row, 2 smooth and 2 pinnate setae. Basis with 2 endites; proximal endite largest, with spinules near distal margin, 1 short subapical seta and 3 elements (1 bare, 2 pinnate) apically, distal endite small, with 1 short plumose seta and 1 long, bare seta. Rami lobate, each with long setules around outer margin, 2 bare setae apically and 1 plumose inner seta subapically.

Maxilla (Fig. 4C) with 3 endites on syncoxa; proximal endite bilobate, with inflated spine and bipinnate tube-seta on proximal lobe and plumose, basally enlarged seta on distal lobe; middle and proximal endites each with 3 ornamented spines (innermost on middle endite fused at base). Allobasis drawn out into bipinnate claw (original articulation marked by basal membranous insert; accessory armature consisting of 1 weakly geniculate and 2 bare setae. Endopod completely incorporated into allobasis, represented by 1 bipinnate and 2 bare setae arising from membranous area.

Maxilliped (Fig. 4D, E) arising from membranous pedestal bearing tiny spinules along outer margin. Syncoxa elongate, with posterior and anterior spinule row near base and anterior spinule row plus pinnate seta near articulation with basis. Outer margin of basis with 2 spinular tufts; palmar margin excavate, with double row of large spinules anteriorly (Fig. 4D); armature consisting of densely pinnate spinulose pad arising from concavity and short tube-seta originating from posterior margin. Endopod drawn out into robust, naked claw; accessory armature consisting anteriorly of 2 slender naked setae and 1 nonarticulating minutely pinnate spine, posteriorly of a nonarticulating, abruptly tapering, pinnate spike.

P1 (Fig. 5A–C). Praecoxa and intercoxal sclerite bare. Coxa with minute spinules on anterior surface and large spinules along outer margin. Basis with anterior surface spinule row and along inner margin; additional spinules present around bases of inner and outer spines; outer spine stout and bipinnate; inner spine slender and bipinnate. Exopod 3-segmented; exp-1 elongate, with spinules around along outer margin and around insertion of outer spine (posteriormost very large); exp-2 elongate, with membranous insert at proximal inner margin and spinules along proximal two-thirds of outer margin, inner seta bare, outer spine short; exp-3 represented by small sclerite partly embedded in membranous proximal part of exp-2 (Fig. 5B), with one geniculate claw and 2 short plus 2 long non-geniculate claws, all claws minutely bipinnate (not shown in Fig. 5B). Endopod slightly longer than exp-1, 2-segmented; enp-1 elongate, with spinules along inner, outer, and distal margins, inner seta multipinnate and reaching just beyond distal margin of enp-2; enp-2 (Fig. 5C) forming distinct condylar joint, outer margin with 2 spinular combs, proximal one distinctly graded, armature consisting of 1 geniculate claw, 1 nongeniculate claw, and 1 bare seta distally, and 1 bare seta laterally; endopodal claws minutely bipinnate (not figured in Fig. 5C).

P2 (Fig. 6A) with bare intercoxal sclerite. Ornamentation of protopodal segments and exopod as figured; basis with outer bipinnate spine. Endopod modified, 3-segmented; enp-1 elongate with spinules along outer margin and plumose inner seta; enp-2 with long outer spinous apophysis, being 3 times as long as enp-3, and with pinnate inner seta; enp-3 small, with spinules along outer margin, armature comprising 2 plumose inner setae, a short, sparsely pinnate inner distal seta and a long, tripinnate outer distal seta.

P3 (Fig. 5D, E). Basis with outer seta. Exopod modified, 3-segmented, slightly inwardly bent; all segments robust, broad; inner setae of exp-1 and -2 and proximalmost of exp-3 short; exp-1 and -2 with strong outer spine; exp-3 with 3 enlarged, minutely pinnate outer spines, 1 long pinnate spine and seta distally, and 3 plumose

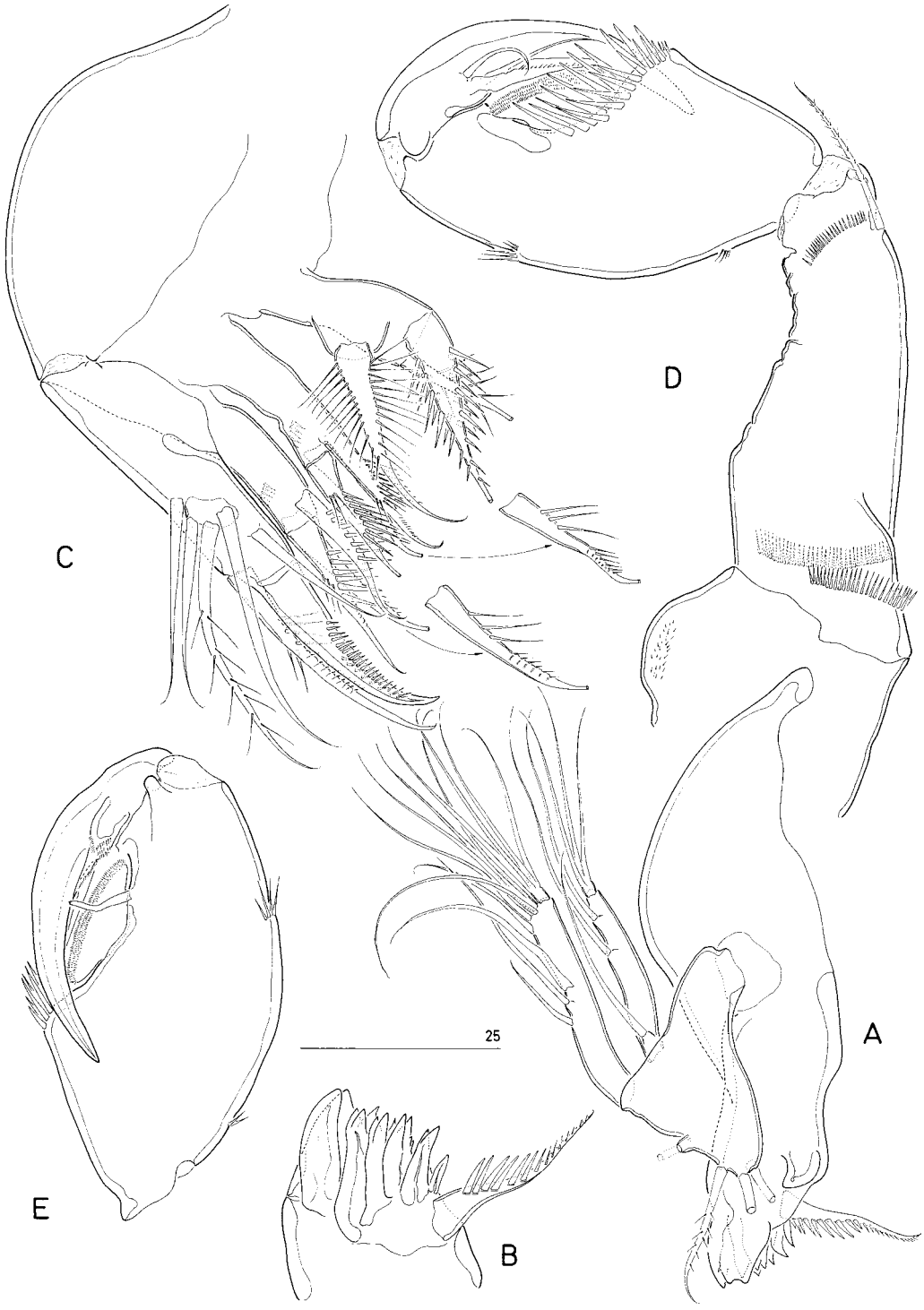


Fig. 4. *Harpacticus spartacus* (Leigh-Sharpe, 1936), new combination (♂). A, Mandible; B, Mandibular gnathobase; C, Maxilla; D, Maxilliped, anterior; E, Maxillipedal basis and endopod, posterior.

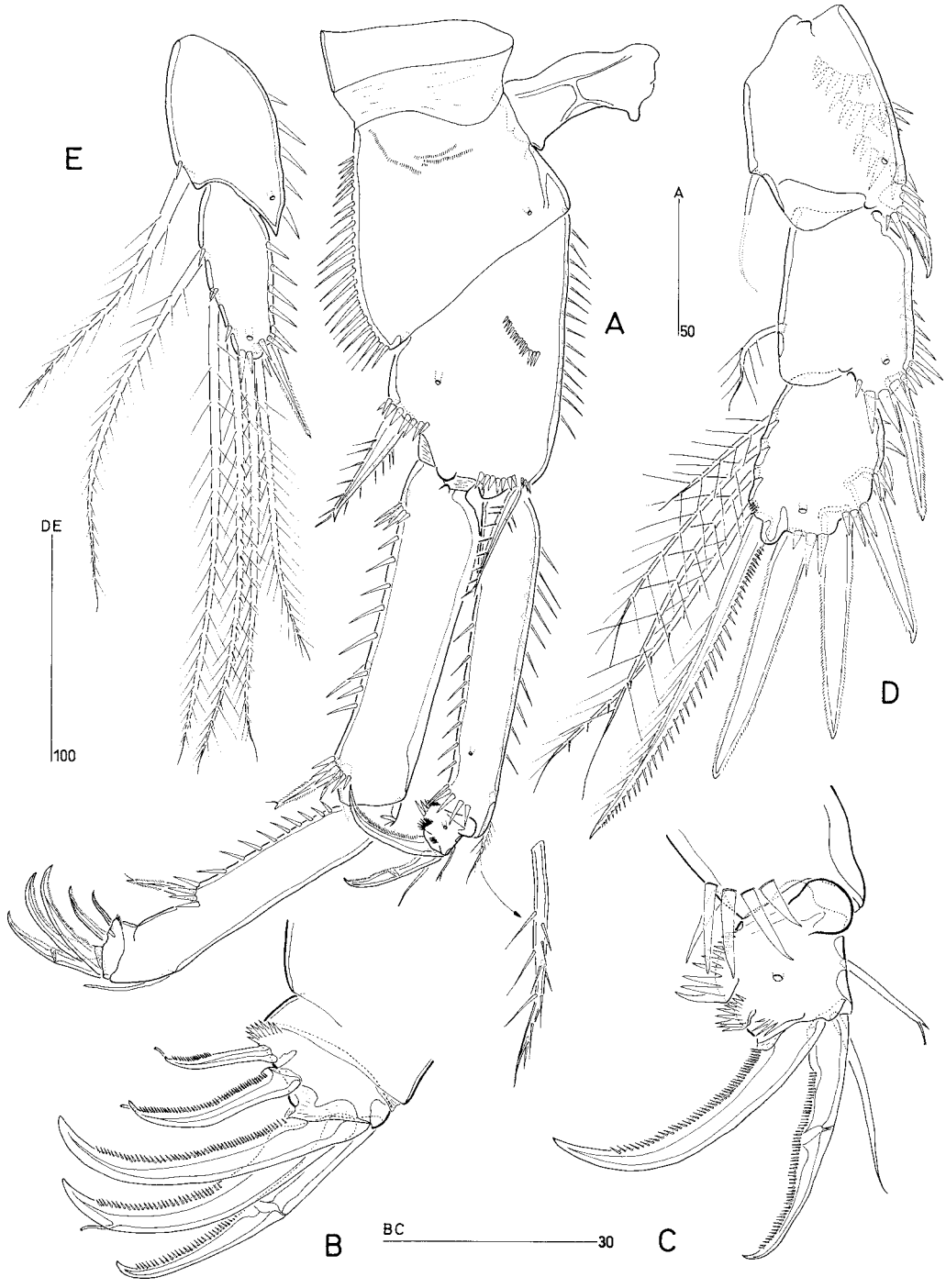


Fig. 5. *Harpacticus spartacus* (Leigh-Sharpe, 1936), new combination (♂). A, P1, anterior [insert showing inner seta of enp-1]; B, P1 exp-3, anterior; C, P1 enp-2, anterior; D, P3 exopod, anterior; E, P3 enp-2 and -3, anterior.

setae along inner margin. Endopod 3-segmented; outer distal angle of enp-2 attenuated (Fig. 5E).

P4 as figured in Fig. 6B.

Armature formula of P2–P4 as follows:

| | Exopod | Endopod |
|---|---|---|
| P2 | 1.1.223 | 1.1.220 [modified] |
| P3 | 1.1.323 | 1.1.321 |
| P4 | 1.1.323 | 1.1.221 |

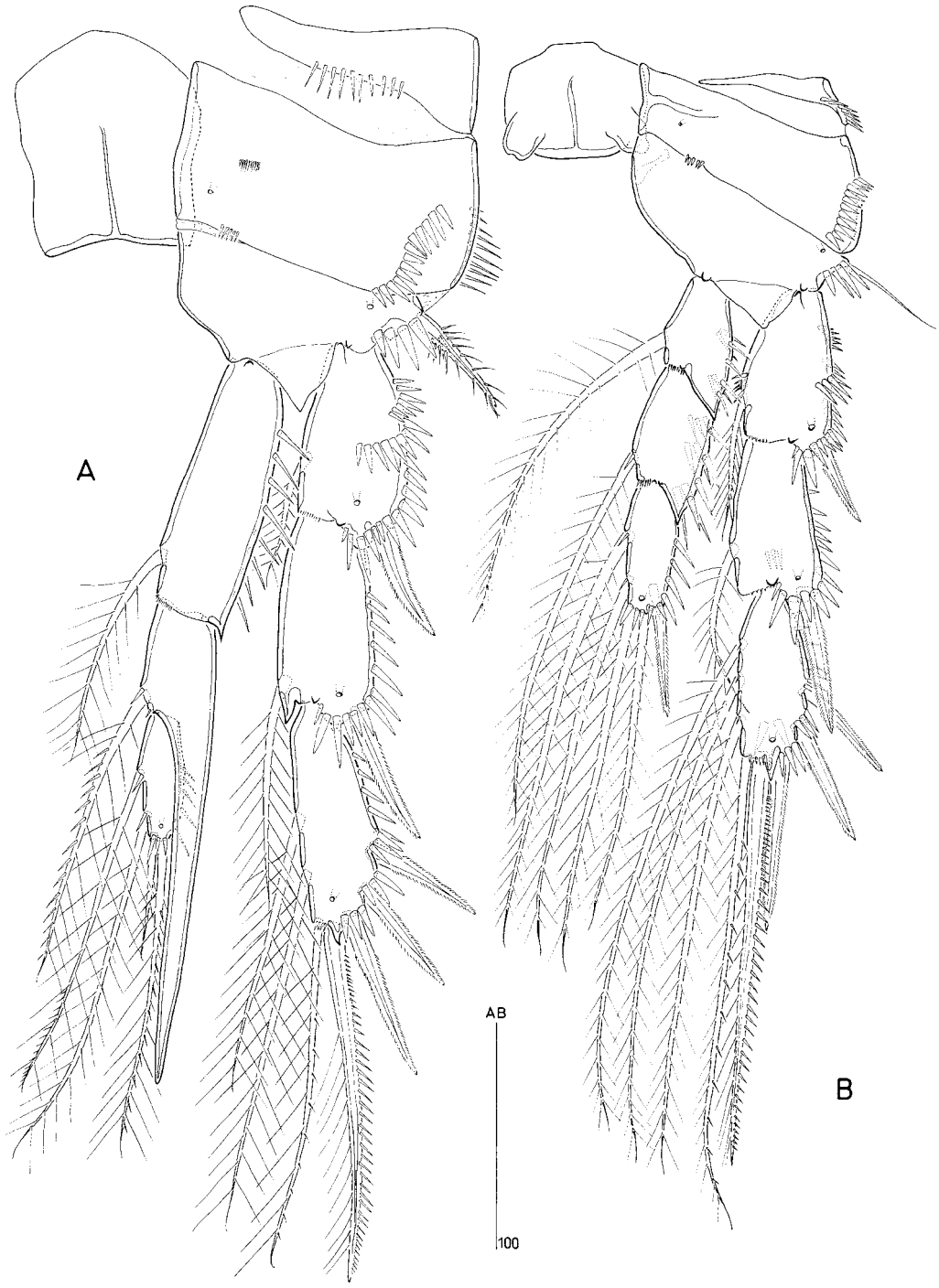


Fig. 6. *Harpacticus spartacus* (Leigh-Sharpe, 1936), new combination (♂). A, P2, anterior; B, P4, anterior.

Fifth pair of legs fused to somite with exopods remaining free (Figs. 1C, 3D, 7C). Outer basal seta smooth, arising from short setophore surrounded by spinules. Exopod outer margin convex, not markedly stepped; with 3 strong, minutely bipinnate spines (with subapical tubular extension) and various spinular patches as figured. Apex of exopod with

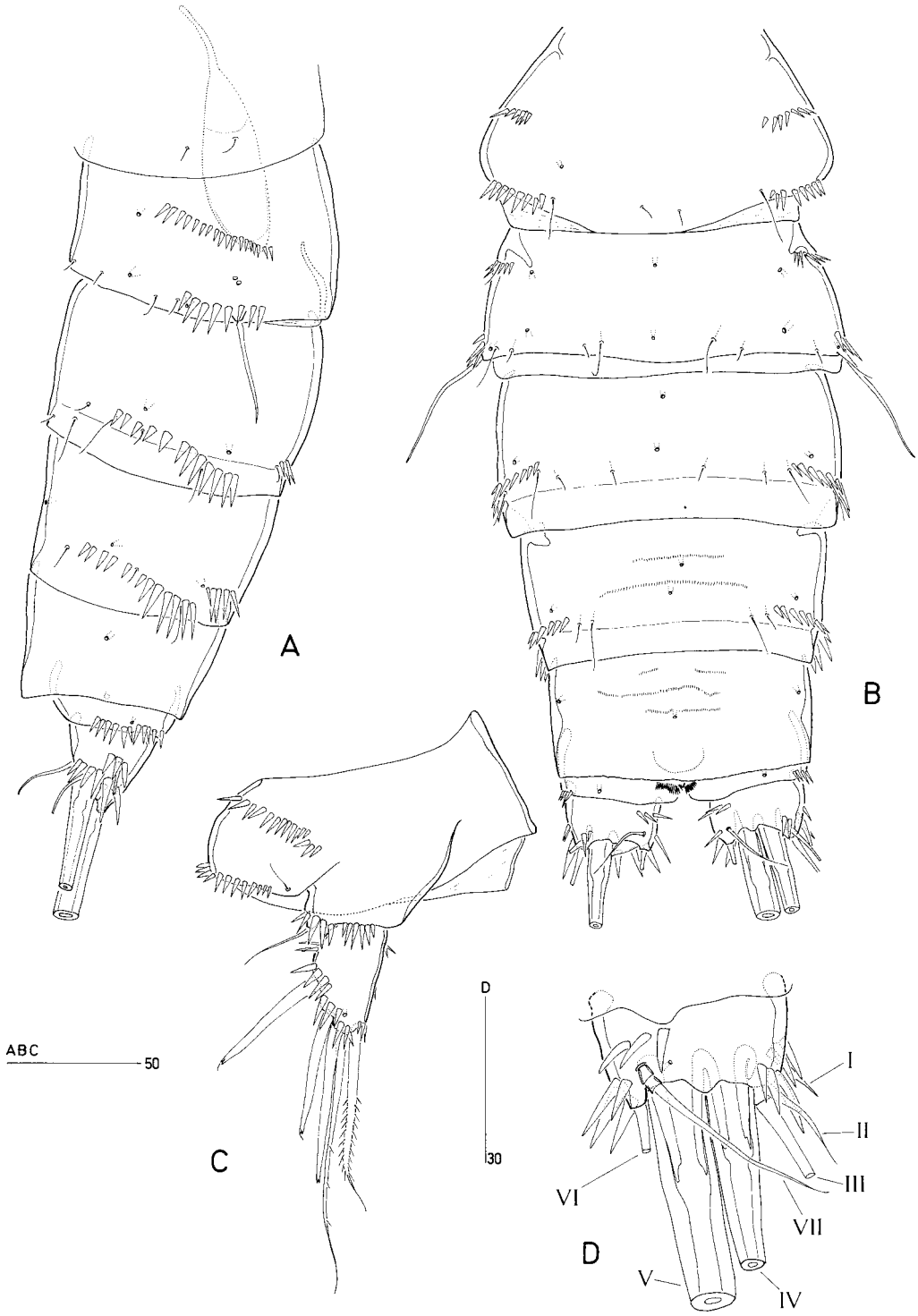


Fig. 7. *Harpacticus spartacus* (Leigh-Sharpe, 1936), new combination (♂). A, Urosome (excluding P5-bearing somite), lateral; B, Urosome, dorsal; C, P5-bearing somite, lateral; D, Right caudal ramus, dorsal.

Table 1. Summary of nomenclatural changes pertaining to *Harpacticus gracilis*, *H. nicaeensis*, and *H. spartacus*, new combination.

| Original name | Current name or status |
|---|---|
| *H. gracilis* Claus, 1863 | *species inquirenda* |
| *H. gracilis* Claus, 1863, *sensu* Sars (1904) | amalgamate of *H. giesbrechti* and *H. obscurus* |
| *H. gracilis* Claus, 1863, *sensu* Monard (1926, 1928) | *H. longiantennata* Apostolov and Petkovski, 1980 |
| *H. elongatus* Boeck, 1865 | *species inquirenda* |
| *H. dentatus* Krichagin, 1873 | *species inquirenda* |
| *H. fucicolus* T. Scott, 1912 | *species inquirenda* |
| *H. nicaeensis* Claus, 1866 ["stärkeren Form"] | *H. nicaeensis* Claus, 1866 |
| *H. nicaeensis* Claus, 1866 ["stärkeren Form" *sensu* Steuer (1937)] | *H. nicaeensis* Claus, 1866 |
| *H. nicaeensis* Claus, 1866, var. *pontica* Czerniavski, 1873 | *H. nicaeensis* Claus, 1866 |
| *H. aegialobates* Monard, 1926 | *H. nicaeensis* Claus, 1866 |
| *H. pulvinatus* Brady, 1910, *sensu* Petkovski (1964) | *H. nicaeensis* Claus, 1866 |
| *H. nicaeensis* Claus, 1866, *sensu* Candeias (1959) | *species inquirenda* |
| *Ismardis spartacus* Leigh-Sharpe, 1936 | *H. spartacus* (Leigh-Sharpe, 1936), new combination |
| *H. nicaeensis* Claus, 1866 ["schwächeren Form"] | *H. spartacus* (Leigh-Sharpe, 1936), new combination |
| *H. nicaeensis* Claus, 1866 ["schwächeren Form" *sensu* Steuer (1937)] | *H. spartacus* (Leigh-Sharpe, 1936), new combination |

long, slender, sparsely pinnate seta; inner margin with subdistal bipinnate seta and few spinules.

Sixth pair of legs symmetrical, fused to genital somite; armature consisting of single smooth seta (Figs. 3D, 7A).

Spermatophore elongate-oval; length 90 μm.

## Discussion

Leigh-Sharpe (1936) recognized a superficial resemblance between *Ismardis* and *Pseudothalestris* Brady, 1883, a junior subjective synonym of *Diarthrodes* Thomson, 1882; however, he regarded the many differences in the appendages as an insurmountable obstacle to inclusion in the Thalestridae. Lang (1948) severely criticized Leigh-Sharpe's description of *I. spartacus*, pointing out inconsistencies in the text with regard to the segmentation of the swimming legs and questioning the sexual dimorphism of the antennae. The latter was clearly caused by accidentally superimposing the right and left antennary endopod in the male. Lang nevertheless was of the opinion that the Ismardiidae should almost certainly sink as a junior synonym of the Thalestridae, but it was probably the many errors in Leigh-Sharpe's illustrations that prevented him from doing so. Neither Lang nor Leigh-Sharpe recognized that the description of the female was in reality based on a copepodid IV.

The present redescription, revealing the correct morphology of the P1 (both rami prehensile) and the sexual dimorphism of the P2 endopod, unequivocally demonstrates that the genus *Ismardis* should be transferred to the family Harpacticidae, the Ismardiidae becoming therefore a junior synonym of the latter. The Harpacticidae currently accommodates 12 genera (Huys *et al.*, 1996; Bouck *et al.*, 1999). The swimming leg setation and segmentation, the presence of sexual dimorphism on the P2 endopod, and the 2-segmented antennary exopod clearly identify *I. spartacus* as a member of *Harpacticus*, and *Ismardis* should consequently be relegated to a junior synonym of this speciose genus.

Various other *Harpacticus* species have their type locality in the Mediterranean, including *H. gracilis* Claus, 1863 (Messina, Italy); *H. nicaeensis* Claus, 1866 (Nice, France); *H. compsonyx* Monard, 1926 (Banyuls-sur-Mer, France); *H. longiantennata* Apostolov and Petkovski, 1980 (Rovinj, Croatia); and *H. flexulosus* Ceccherelli, 1988 (Po River delta, Italy). The inadequate original desciptions of *H. gracilis* and *H. nicaeensis* have caused tremendous taxonomic confusion. The intricate taxonomic history of these species is unravelled below in order to confirm the identity of *H. spartacus* (see also Table 1).

### *Harpacticus gracilis*

Claus (1863) figured only the female antennule of *H. gracilis*, and his text description contains virtually nothing of diagnostic value, making the species practically unidentifiable. Klie (1927) suggested to rank it *species inquirenda*, but his opinion was not followed by subsequent authors. This was partly due to Sars (1904), who

had set the standard by figuring in considerable detail what he considered to be *H. gracilis* in Norwegian waters, and to Lang (1948), who considered *H. gracilis* a very variable species. Lang (1948) re-examined Sars' material and rightly concluded that his illustrations of the male were based on an aberrant specimen. Aberrations are particularly evident in the P3 exopod, showing the three outer spines on exp-3 gradually shortening instead of increasing in length as in every other member of the genus, and in the P5 exopod which displays two atypically curved outer spines. Lang concluded that both legs are identical to those figured by Giesbrecht (1882) for what he had identified as *H. chelifer* (O. F. Müller, 1776) from Kiel Bay and was later renamed *H. giesbrechti* by Klie (1927). Having accepted the conspecificity between Sars' "*gracilis*" and Giesbrecht's "*chelifer*" as Sars (1904) had done before, Lang (1948) relegated *H. giesbrechti* to a junior synonym of *H. gracilis sensu* Sars (1904), but Huys *et al.* (1996) reinstated the former as a valid species within the *obscurus*-complex. Although Sars' illustrations do not provide the detail required for species discrimination within the *obscurus*-group (see Huys *et al.* (1996) for examples of diagnostic characters used to separate closely related NW European species), they give one indication that at least the female figured belonged to a species different from *H. giesbrechti*. His drawing of the P5 exopod shows the second outer seta to be markedly shorter than the proximalmost one, a feature characteristic of *H. obscurus* T. Scott, 1895 (Huys *et al.*, 1996: fig. 113D) but never expressed in *H. giesbrechti* (Giesbrecht, 1882: fig. XII-24) in which both elements are of similar length. We have re-examined Sars' (1904) material (ZMO reg. no. F16849; precise locality unknown) and found it to contain an amalgamate of two species, differing consistently in size and in several minute characters related to ornamentation and morphometry. In females of the smaller species (around 0.65 mm), here identified as *H. giesbrechti*, the inner seta of P1 enp-1 is sparsely bipinnate and reaching to about the tip of the nongeniculate claw of enp-2, the P1 enp-2 has a pore in the middle of the anterior surface, the P3 enp-2 has two pores near the distal outer corner, and the P5 baseoendopod has a pore near the inner margin and a seemingly straight distal margin giving a truncated appearance to the endopodal lobe. In the larger females (around 0.9 mm), here identified as *H. obscurus*, the inner seta of P1 enp-1 is moderately densely tripinnate and reaching only slightly beyond the distal margin of enp-2, the P1 enp-2 lacks pores on the anterior surface, the P3 enp-2 has only 1 pore near the distal outer corner, and the P5 baseoendopod has no pore near the inner margin and a more rounded distal margin. Additionally, in *H. giesbrechti*, the claws on P1 exp-3 are longer, straighter, and have generally a finer pectination, P2 enp-1 is distinctly shorter and the P5 exopod is more elongate-oval than in *H. obscurus*. In addition to the P1 characters, males attributable to *H. giesbrechti* can be differentiated by the presence of an oblique lateral spinule row on either side of the genital somite and by the much shorter spinous apophysis on P2 enp-2. Sars (1904) and Lang (1948) cite *H. elongatus* Boeck, 1865 as a junior synonym of *H. gracilis*, but this course of action is clearly unsubstantiated because Boeck's (1865) description is completely lacking in illustrations. Dr R. Hamond has informed us that the only sample labelled *H. elongatus* by G.O. Sars (ZMO reg. no F16841) contains in reality *H. obscurus*. This leaves open the possibility that *H. elongatus* is the senior synonym of *H. obscurus* (or even *H. giesbrechti* or *H. littoralis* Sars, 1910), but pending re-examination of specimens from Boeck's type locality (which is equally as vague as his description), we rank the former as *species inquirenda*.

Lang (1948) admitted that his decision to consider *H. gracilis* a highly variable species was primarily based on his observations of Sars' (1904) material. His inability to distinguish between *H. obscurus* and *H. giesbrechti* is reflected in the variability noted by him in the ornamentation of the claws on P1 exp-3 and the shape of the P5 exopod. Conversely, the variability observed in the number and form of elements on P1 exp-3 is conceivably either the result of the deficient condition of most of Sars' material or due to imperfect observation. Although Lang (1948) did not entirely exclude the possibility of *H. gracilis* being a species complex, he found it more logical to consider it a morphologically plastic species, a view already asserted by Jakubisiak (1938) who called it an "espèce collective." Consequently, Lang (1948) subsumed various other species under the name *H. gracilis* based either on re-examination of original material (*H. gracilis sensu* Monard (1926), *H. nicaeensis* - "schwächeren Form" of Steuer (1937)) or reinterpretation of original

descriptions (*H. gracilis sensu* Claus (1863); *H. dentatus* Krichagin, 1873; *H. fucicolus* T. Scott, 1912; *H. nicaeensis* - "schwächeren Form" of Claus (1866); *H. nicaeensis* var. *pontica* Czerniavski, 1868).

Monard (1926, 1928) attributed several specimens from Banyuls to *H. gracilis* and based his identification on the elongated form of the antennule, maxilliped, and P1. The validity of the latter two characters is hard to quantify because Claus (1863) did not figure these appendages; however, his illustration of the antennule shows distinct differences in the proportional lengths of segments 3–4 with Monard's (1926, 1928) material. In fact, *H. gracilis* resembles more closely the specimens identified by Monard as *H. littoralis* (his fig. 7). *Harpacticus littoralis*, which was originally described from the west and south coasts of Norway (Sars, 1910), is one of the larger species in the genus (around 1–1.1 mm) and is morphologically very close to *H. obscurus* and *H. giesbrechti* (Huys *et al.*, 1996). There are at present no confirmed records of *H. littoralis* from the Mediterranean, its distribution being restricted to northwest Europe as far south as Brittany. Monard's specimens measured only 0.6–0.7 mm, which agrees with the female body length given by Claus (1863). They also differ from genuine *H. littoralis* in the following respects: (1) the inner seta of P1 enp-1 is much shorter, only reaching to the distal margin of enp-2 (instead of extending to the tip of the nongeniculate claw), (2) the ♀ P5 exopod is distinctly longer; and (3) the endopodal lobe of ♀ P5 has an angular outline and is narrower (instead of having a straight distal margin with all setae, except the innermost, arranged at the same level across it). Lang (1948) re-examined two specimens and remarked that the P5 exopod is in reality less slender, probably because Monard viewed it under a different angle. It is conceivable that the *H. littoralis* material from Banyuls represents an undescribed species in the *obscurus*-complex; however, its conspecificity with Claus' (1863) *H. gracilis* can neither be authenticated nor refuted. Conversely, Monard's (1926, 1928) *H. gracilis* is clearly identical to *H. longiantennata*, described by Apostolov and Petkovski (1980) from the northern Adriatic Sea. The most conspicuous character of this species is the extreme elongation of segments 3–4 and 6 of the female antennule. Monard's (1928) illustrations agree in every aspect with Apostolov and Petkovski's (1980) description, except for the male P2 endopod which has a distinctly shorter spinous apophysis in the Banyuls material; however, it is known that this character can display significant variation in some species such as *H. giesbrechti*.

Krichagin's (1873) illustrations of *H. dentatus* from the eastern Black Sea severely lack detail and show several inconsistencies (e.g., the 10-segmented antennule in the female), which does not inspire confidence in their accuracy. It is incomprehensible why Lang (1948) uncritically accepted this species as a synonym of *H. gracilis* because no positive statement can be made as to the validity of either of them. We agree with Gurney (1927) that *H. dentatus* is unrecognizable and rank it *species inquirenda* within the genus.

Scott (1912) described *H. fucicolus* from floating seaweed collected in the North Atlantic between the Cape Verde Islands and the Azores. His description is too concise for any positive statement to be made on the identity of this species. Scott himself admitted that *H. fucicolus* may well turn out to be conspecific with *H. gracilis*, a suggestion adopted by Gurney (1927) and subsequently confirmed by Lang (1948) who formalized the synonymy. However, in view of the taxonomic confusion surrounding *H. gracilis* and provided that Scott's (1912) illustration of the antennary exopod is correct (only *H. flexus* has a similarly reduced armature on this ramus), we regard it premature to relegate *H. fucicolus* to a junior synonym of the latter and prefer to consider it a *species inquirenda*. Monard (1935) reported *H. fucicolus* from the Salammbô region in Tunisia, but it is impossible to decide whether this record really refers to *H. gracilis* as Lang (1948) surmised.

In summary, because Claus' (1863) description of *H. gracilis* is valueless for identification purposes, all subsequent records referring to this species have to be considered at least unconfirmed, if not doubtful or false. Only the collection of topotype material may shed light on the true identity of this allegedly cosmopolitan species.

### *Harpacticus nicaeensis*

Claus (1866) recognized two varieties of *H. nicaeensis* in his material from Nice. The robust ("stärkeren Form") variety he regarded closer to *H. chelifer* whilst the slender ("schwächeren Form") form he considered particularly close to

his *H. gracilis* from Messina. The latter form differed from the robust one in a number of predominantly meristic characters such as the longer and narrower rostrum, the more elongate antennule (segments 3–4 distinctly longer), the more slender maxillipedal claw, and the number of elements on P1 exp-3.

Despite the information content of Claus' (1866) original description being higher than that of *H. gracilis* (cf. Claus, 1863), *H. nicaeensis* has for a long time been considered an invalid species, being synonymized at various occasions with other species. Car (1890) synonymized *H. nicaeensis* with *H. chelifer* but gave no explanation supporting his course of action. Brian (1919, 1921) considered *H. nicaeensis* as a probable synonym of *H. uniremis* Krøyer, 1842, whilst Gurney (1927) regarded *H. nicaeensis* and *H. gracilis* as conspecific because in his opinion no satisfactory discriminating characters appeared to exist between both species. Monard (1926) pointed out that the concise original descriptions rendered Claus' (1866) varieties of *H. nicaeensis* unidentifiable.

Monard (1926) described a new species, *H. aegialobates*, which according to Brian (1928) is identical to Claus' (1866) "stärkeren Form" of *H. nicaeensis* (but Monard (1935) questioned this synonymy) and to his own material previously misidentified as *H. uniremis* (Brian, 1919, 1921, and possibly 1923—see Steuer (1937)). Surprisingly, Brian retained the junior name *H. aegialobates* instead of *H. nicaeensis*, which takes priority. Monard (1928), in his study on the harpacticoids from Banyuls, appeared to regard *H. nicaeensis* as a synonym of *H. gracilis* because he cited Nice as the only additional French Mediterranean record, but in a later report (Monard, 1936), he treated the former merely as a *nomen nudum*. Steuer (1937) criticized Claus' (1866) fragmentary descriptions but nevertheless claimed that there was sufficient morphological evidence to maintain both morphotypes of *H. nicaeensis*. He described two forms that co-occurred in a sample taken off Sidi Bishr near Alexandria, Egypt, and listed conspicuous differences in the rostrum, abdominal spinulation patterns, maxilliped, and P1.

Lang (1948) re-examined Steuer's material and concluded that both varieties represented distinct species, differing in rostrum shape, the form of the elements on the distal endopod segment of P1, and the shape of the ♀ P5 exopod. The "stärkeren Form" of both Claus (1863) and Steuer (1937) he equated with genuine *H. nicaeensis* (following Claus' (1863) page priority)) and, in accordance with previous authors (Brian, 1928; Steuer, 1937), treated *H. aegialobates* as a junior subjective synonym of the latter. As pointed out by Steuer (1937), the robust form is most readily distinguished by its P1 endopod, which is about as long as the proximal exopod segment and has a characteristic, slightly upwardly recurved outer spike on the distal segment. The latter character is not an armature element but an elaboration of the proximal spinular comb found in other *Harpacticus* species. This character is so distinctive that it was even figured by Claus' (1866) otherwise deficient description of *H. nicaeensis* and serves as a reliable reference feature to confirm other figured records of the species. There is no doubt that *H. aegialobates* is conspecific with *H. nicaeensis* because Monard (1926, 1928) shows exactly the same structure. Raibaut (1962) resurrected *H. aegialobates* using the alleged presence of smooth spines on the antennary endopod in *H. nicaeensis* as the sole discriminant; however, this statement must be a misinterpretation because both Czerniavski (1868) and Petkovski (1964; as *H. pulvinatus* Brady, 1910—see below) illustrate pinnate spines (and Steuer (1937) mentioned them in the text description), as in *H. aegialobates*. Raibaut also remarked that his specimens had not five (as reported by Monard (1926, 1928)) but six elements on P3 enp-3, but he regarded this difference as insignificant. It is obvious that Monard made an observational error because all *Harpacticus* species possess six elements on this segment.

*Harpacticus nicaeensis* appears to be common in the western Mediterranean; however, Steuer's (1937) record from Egypt suggests that its distribution extends to the easternmost part of this basin. The only reliable record outside the Mediterranean is that by Petkovski (1964), who erroneously identified it as *H. pulvinatus* from Portugal. The latter is morphologically quite different from *H. nicaeensis* (see Lang, 1934; Pallares, 1968, 1973) and is restricted to high latitudes in the Southern Hemisphere with records from the South Orkneys, Kerguelen, Macquarie Island, Stewart Island, and southern Argentina. Likewise, Apostolov's (1970) unillustrated record of *H. pulvinatus* (which is not listed in Apostolov and Marinov's (1988) catalogue) along the Bulgarian coast is equally doubtful.

There are several records of *H. nicaeensis* from the Black Sea basin including the coasts of Bulgaria (Chichkov, 1912; Valkanov, 1957; Naidenov, 1966; Michailova-Neikova, 1968; Apostolov, 1970; Michailova-Neikova and Voinova-Stavreva, 1971; Apostolov and Marinov, 1988) and Ukraine (Czerniavski, 1868; Grebnitskii, 1873; Marcus and Por, 1960). Many of these reports cannot be authenticated, but of those that are accompanied by illustrations, Apostolov and Marinov's (1988) from Bulgaria and Czerniavski's (1868) from Yalta can be regarded as reasonably reliable because both show the spike on P1 enp-1 and agree in most other aspects with Steuer's (1937) account. Czerniavski (1868) established a separate variety for the Ukrainian specimens, which he named *H. nicaeensis fortior* var. *pontica*, but there are no morphological grounds for either maintaining this distinction (Marcus and Por, 1960; Mordukhai-Boltovskoi, 1969) or substantiating Lang's (1948) claim to subsume this variety under *H. gracilis*. Note that Czerniavski's illustration of the male P3 exopod is incorrect because it shows five enlarged spines on the distal segment rather than the typical three. The Yalta material illustrated by Marcus and Por (1960) clearly does not belong to *H. nicaeensis* because it differs markedly in the P1 and female P5. It is conceivable that one of the claws on P1 enp-2 was broken off during dissection and that the inner setae on P3 exp-1 and -2 were overlooked.

Of the few records of *H. nicaeensis* outside the Ponto-Mediterranean basin, those of Brady (1872) from the Durham coast (U.K.) were regarded as uncertain and probably false by Lang (1948). Brady did not provide any figures and seemed to have abandoned this record altogether in his *Ray Society* volumes on the British Copepoda (Brady, 1880). Candeias (1959) attributed specimens from Angola to the robust form of *H. nicaeensis* but remarked that the similarity was not absolute. The Angolese males differ in the proportional lengths of the elements on the P5 exopod (which itself is also more slender and longer than in Steuer's (1937) description) and the comparatively longer spines on the P3 exopod. As pointed out by Candeias, the maxilliped is comparatively stronger, but this discrepancy is negligible in our opinion. More important are the individual size differences of the claws on the distal segment of the P1 exopod, and to a lesser extent, the endopod. The presence of a conspicuous spike on P1 enp-2 leaves little doubt that Candeias' material is closely related to *H. nicaeensis*. In the absence of voucher specimens, it seems, however, premature to establish a new species for the Angolese specimens; at present, we prefer to treat *H. nicaeensis sensu* Candeias (1959) as *species inquirenda* and regard it as circumstantial evidence for the existence of a *nicaeensis*-complex. *Harpacticus pulex*, described by Humes (1964) from sloughed skin tissue of the porpoise *Tursiops truncatus* (Montague) and the manatee *Trichechus manatus latirostris* (Harlan), probably also belongs to this complex by virtue of the presence of two spike-like structures (derived from both proximal and distal spinule combs!) on P1 enp-2.

*Harpacticus spartacus*, new combination

The "schwächeren Form" was diagnosed by Steuer (1937) on the basis of the following characters: (1) female rostrum longer and narrower than in the robust variety; (2) the lack of middorsal spinules around the hind margin of second and third abdominal somites; (3) female antennule with segments 3–4 largest and equally long, segment 6 also more elongate than usual; (4) P1 exp-3 with 2 small and 3 large claws; (5) P1 enp-2 without conspicuous spike but with graded series of spinules. Steuer (1937) also illustrated differences with the robust form in the robustness of the maxilliped and the length of the male P5 exopod but did not explicitly discuss them. The male of *H. spartacus* resembles Steuer's slender form very closely, particularly in the detailed morphology of the P1 (i.e., the relative size of the claws on exp-3 (Fig. 5B) and the steeply graded spinule comb on enp-2 (Fig. 5C)); the maxilliped (long and slender syncoxa; Fig. 4D); the rostrum (Fig. 1B); the male P5 (Fig. 1C); and in the absence of middorsal spinules on abdominal somites 2–3 (Figs. 1A, 7A, B). On the basis of this suite of characters, the slender variety of both Claus (1866) and Steuer (1937) is regarded here as conspecific with *H. spartacus*, rejecting Lang's (1948) claim that it represented just another form of the "polymorphic" *H. gracilis*. *Harpacticus spartacus* belongs to the *obscurus*-complex and is probably most closely related to *H. giesbrechti*. It can be differentiated from this species by (1) the length of the inner seta on P1 exp-2 being much shorter and tripinnate instead of sparsely bipinnate; (2) the different form of the proximal spinular comb on P1 enp-2 (not or weakly graded in *H. giesbrechti*); and (3) male

P5 exopod being distinctly shorter and with relatively straight outer margin (distinctly stepped at level of proximalmost outer spine in *H. giesbrechti*). The reliable records (Claus, 1866; Leigh-Sharpe, 1936; Steuer, 1937) suggest that *H. spartacus* is distributed throughout the Mediterranean from the French coast in the west to Egypt in the east and that its discovery in a patellid was merely a chance association or contamination (Leigh-Sharpe did not extract the copepods himself). There are no confirmed literature records from the Black Sea.

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