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A taxonomic revision of European *Herpetocypris* BRADY and NORMAN, 1889 (Crustacea, Ostracoda)

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Abstract

The European representatives of the genus *Herpetocypris* are revised, based on extant type material and various new collections. The revision is based on the hypothesis that species with syngamic populations will show large intra-specific morphological variability and that parthenogenetic taxa will have both less intra-specific variability and small morphological differences between taxa. Of the nearly 20 extant nominal species, subspecies and varieties, 6 recent species are retained.
Herpetocypris reptans, with both the common nominal subspecies and *H. reptans curvata* (known from its type locality only), occurs in most of Europe, north of the Mediterranean. *Herpetocypris brevicaudata* is the only species in which syngamic populations occur, these are thus far only found in the western part of the Mediterranean. Parthenogenetic populations occur throughout Europe. This species shows larger morphological variability. *Herpetocypris mateusorum* is confined to western Iberia. *Herpetocypris chevreuxi-intermedia-helenae* form a closely related species cluster, which occurs throughout Europe, at least *H. helenae* appears to have a global distribution.
Some morphological peculiarities of this genus are discussed, as is the variability in several of the so-called diagnostic characters. Some remarks on the evolution in this genus are offered.
Key words: Taxonomy, morphology, distribution, reproductive modes, syngamy, parthenogenesis.

Résumé

Les représentants européens du genre *Herpetocypris* sont révisés, sur la base du matériel-type existant et de diverses nouvelles collections. La révision est basée sur l'hypothèse que les espèces ayant des populations syngamiques ont une plus grande variabilité morphologique intra-spécifique et que les taxa parthénogénétiques présentent à la fois une plus petite variabilité intra-spécifique et des différences morphologiques peu prononcées entre les taxa. Parmi les quelque 20 espèces, sous-espèces et variétés nominales existantes, 6 espèces récentes sont retenues. *Herpetocypris reptans*, avec aussi bien la sous-espèce nominale commune, que *H. reptans curvata* (connu uniquement de sa localité-type), apparaît dans la majeure partie de l'Europe, au nord de la Méditerranée. *Herpetocypris brevicaudata* est la seule espèce présentant des populations syngamiques, rencontrées jusqu'à présent uniquement dans la partie occidentale de la Méditerranée. Des populations parthénogénétiques vivent dans toute l'Europe. Cette espèce présente une plus grande variabilité morphologique. *Herpetocypris mateusorum* est limité à l'Ibérie occidentale. *Herpetocypris chevreuxi-intermedia-helenae* est un groupe d'espèces très proches et que l'on rencontre dans toute l'Europe, au moins *H. helenae* a apparemment une distribution globale.
Certaines particularités morphologiques de ce genre sont discutées, de même que la variabilité de plusieurs "caractères diagnostiques". Quelques remarques sur l'évolution de ce genre sont proposées.
Mots-clefs: Taxonomie, morphologie, distribution, modes de reproduction, syngamie, parthénogénèse.

Introduction

The genus *Herpetocypris* BRADY & NORMAN, 1889 is common in small to medium-sized waterbodies and has thus far been reported from Eurasia, North and South America and northern and southern Africa. In Europe, about 20 species, subspecies and varieties have thus far been described, and most of these have at various occasions been lowered or raised in taxonomic rank or were synonymized. Most taxa have been distinguished on the basis of carapace shape and size, length of natatory setae on A2, length of setae on Mx2-palp and size and number of spines on the ventral margin of the furcal rami. At present, the taxonomy of this genus in Europe is highly confused, especially for the Mediterranean populations, and a revision is urgently required (GONZALEZ MOZO *et al.* 1996).
A European research network, consisting of six laboratories in five countries, has investigated the evolutionary ecology of reproductive modes of the three extant lineages of non-marine ostracods with a variety of techniques: morphological and morphometrical analyses, clonal autecology, starch-gel electrophoresis of allozymes and amplification and automated sequencing of both mitochondrial and nuclear DNA. Although not one of the initially selected network genera, the present taxonomic revision of *Herpetocypris* was conducted in its framework and this for the following reason: (1) the

Cypridoidea constitute 70-80% of the specific diversity in non-marine habitats, and it was thus felt that this group should be investigated on more than one representative; (2) *Herpetocypris* is a classical example of a group with geographically segregated reproductive modes: parthenogenetic populations occur throughout Europe, but bisexual populations are found only around the Mediterranean. (3) Several exclusively parthenogenetic species have been reported.
The present revision is thus functional at several levels: (1) to assess the validity of geographical parthenogenesis in this lineage; (2) to test the applicability of the concept of clonal taxonomy to this lineage and (3) to solve the present taxonomic muddle in this group and to present a workable classification of identifiable units.
The present paper presents the taxonomic and morphological results of the revision. Applicability for geographical parthenogenesis and clonal taxonomy will be more extensively discussed elsewhere.

Material & Methods

1. *List of Museums and collections*

BM	Natural History Museum, London, U.K.
MHNG	Musée d'Histoire naturelle de Genève
KBIN	Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium (O.C. = Ostracod Collection)
MCSN	Museo Civico di Storia Naturale, Firenze
MNIP	Museum für Naturkunde, Institut für Paläontologie, Berlin
ZMB	Zoologisches Museum, Berlin, Germany
ZMO	Zoological Museum, Oslo, Norway

2. *Abbreviations used in text and figures*

A1 = Antennula. A2 = Antenna. Cp = carapace. db = dorsal branch of furcal attachment. dms = dorsal lobe of lateral shield of hemipenis. fl = flange. Fu = furca. H = height of valves. il = inner list. im = inner margin. L = length of valves. lc = line of concrescence. ls = lateral shield of hemipenis. LV = left valve. Md = Mandibula. ms = medial shield of hemipenis. M × 1 = Maxillula. Mx2 = Maxilla. ol = outer list. pfz = primary fused zone. r = Rome organ. RV = right valve. sfz = secondary fused zone. sl = selvage. T1 = first thoracopod. T2 = second thoracopod. vb = ventral branch of furcal attachment. vms = ventral lobe of lateral shield of hemipenis. vm = valve margin.

Chaetotaxy of the limbs follows the model proposed by BROODBAKKER & DANIELOPOL (1982), revised for the A2 by MARTENS (1987).

3. *Material*

The present revision relies on type and non-type materials from museums, as well as on new collections from Europe (Spain, Portugal, Belgium, Italy, England, Switzerland), Israel, Africa (Algeria, St Helena, South Africa), and North America (Canada). A list of these collections is given in an appendix. Lists of synonymies in the text deal with literature on European localities only.

Taxonomic descriptions

Class	Ostracoda, LATREILLE, 1806
Subclass	Podocopa G.W. MÜLLER, 1894
Order	Podocopida SARS, 1866
Surorder	Podocopina SARS, 1866
Infraorder	Cypridocopina JONES, 1901
Superfamily	Cypridoidea BAIRD, 1845
Family	Cyprididae BAIRD, 1845
Subfamily	Herpetocypridinae KAUFMANN, 1900 = Stenocypridinae FERGUSON, 1964

Diagnosis: Large (1-2 mm), mostly elongated and laterally compressed ostracods; marginal valves structures mostly well developed; branched pore canals and marginal septae present in some genera. Antennae in males with claw GM developed into a comb-like structure, with one row of strong teeth. Furcae well developed, symmetrical or asymmetrical; furcal attachment with a triangular basal reinforcement (in some genera only weakly developed). Hemipenis with large and sclerotized bladder-like part 'c' of the labyrinth, post-labyrinthal internal spermiduct with a variable number of additional, circular whorls (1-4).

Extant genera: *Herpetocypris* BRADY & NORMAN, 1889; *Acocypris* VAVRA, 1895; *Stenocypris*, SARS, 1889; *Chrissia* HARTMANN, 1957 (syn.: *Gesa* HARTMANN, 1957); *Parastenocypris* HARTMANN, 1964; *Candonocypris* SARS, 1894; *Ilyodromus* SARS, 1894; *Humphcypris* MARTENS, 1996; *Somalicypris* MARTENS, 1996; *Ampullocypris* DE DECKKER, 1981; *Psychrodromus* DANIELOPOL & MCKENZIE, 1977; *Stenocypria* G.W. MÜLLER, 1901.

Distribution: This group occurs on all continents, except Antarctica. None of the genera, however, is cosmopolitan. Herpetocypris has the widest distribution and occurs on all continents, except for Australia and Antarctica.

Habitat: Representatives of this group are common in all types of habitats, both temporary and permanent, although they are not typical of the former. Some genera are adapted to crenobiontic and even hypogean habitats.

Herpetocypris BRADY & NORMAN, 1889
= *Erpetocypris* BRADY & NORMAN, 1889
= *Siphlocandona* BRADY, 1910
= *Exuocypris* MANDELSTAM, 1956

Type species: *Cypris reptans* BAIRD, 1835

Diagnosis
Valves elongated and laterally compressed, L = 1.5-2.5 mm; LV with largely inwardly displaced selvage and wide fused zone, pore canals straight, marginal septae absent. LV overlapping RV on all sides; this valve with well developed il along anterior, ventral and posterior margin. In closed carapace, valve margin of RV fitting between il and valve margin of LV. Mandibular scars small.
A1 with small Rome organ. Natatory setae on A2 very short to long (beyond tips of claws), but always present. Mx1-palp spatulate, with length about equal to distal width. Seta d2 on T1 about 1.5-2 the length of seta d1. Furca symmetrical, proximal seta present, not claw-like, spines on ramus short and grouped. Furcal attachment with typical basal triangle, and an additional, but weakly built small branch towards the distal part of the main branch. Hemipenis without hook-like process on medial shield.

Remarks: Several species have erroneously been described or transferred to this genus. *Herpetoycpris strigata* KAUFMANN, 1900 and *H. peregrina* KAUFMANN, 1900 (a homonym of *H. peregrina* CRONEBERG, 1894) are synonyms of *Tonnacypris lutaria* (KOCH, 1838). *Herpetocypris tumefacta* KAUFMANN, 1900 is a synonym of *Eucypris pigra* (FISCHER, 1851).

Herpetocypris reptans (BAIRD, 1835)

Herpetocypris reptans reptans (BAIRD, 1835)
(Figs. 1(A-O,T), 2(A,B), 17(P), 18(A-G,J-M),)

1835 *Cypris reptans* n.sp. BAIRD: 99-100. Pl. 3 (11)
1845 *Candona reptans* (BAIRD), 153
1889 *Erpetocypris reptans* (BAIRD), BRADY & NORMAN 23, p. 84, Pl. 13(27)
1890 *Herpetocypris reptans* (BAIRD), SARS 28, p. 17
1900 *Herpetocypris reptans* (BAIRD), KAUFMANN: 282, Pl. 16 (1-3); Pl. 18 (21-26)
1928 non *Erpetocypris reptans* (BAIRD) sensu GAUTHIER, fig. A-M. (= *Herpetocypris brevicaudata*)
1938 *Herpetocypris reptans* (BAIRD), KLIE: 125-126 (419-421)
1947 *Herpetocypris reptans* (BAIRD), ROME, fig. 7-15
1947 non *Herpetocypris reptans* (BAIRD) sensu ROME, fig. 16-20 (= male of *Herpetocypris brevicaudata*)
?1955 *Erpetocypris reptans* (BAIRD) ssp. *aulicae* n. ssp. LÜTTIG: 159, Pl. 18 (1)
1969 *Herpetocypris reptans* (BAIRD), NÜCHTERLEIN: 263-265
1982 *Herpetocypris reptans* (BAIRD), TETART: 162-163, fig. 89-103
1987 *Herpetocypris reptans* (BAIRD), MEISCH: 106-107
1992 *Herpetocypris reptans* (BAIRD), BALTANAS: 431, fig. 5

Type locality: Yetholm Loch, Berwickshire (S.E. Scotland), approximate coordinates: 55°33'N, 02°19'W.

Abbreviated diagnosis: Large species (L = 2.2-2.7 mm), with almost evenly rounded anterior and posterior margins and straight to weakly curved dorsal margin; LV with relatively weak inner list, calcified inner lamella evenly sloping between valve margin and selvage. A2 with 1st n.s. the longest, usually reaching the end of the penultimate segment, n.s. 2-5 of constant length, all equally short (reaching to the middle of that segment), 6th n.s. shorter. Fu with delicate claws; proximal setae longer than in the other species, reaching beyond tip of ramus; ventral margin of ramus set with variable groups of teeth (mostly 4 groups of relatively large teeth and 2 groups with smaller teeth).

Additional description
Largest species in the genus, with anterior and posterior margins evenly rounded and straight to weakly curved dorsal margin; ventral margin straight; LV longer and higher than RV. LV with calcified inner lamella evenly sloping between valve margin and inner list, not forming an abrupt angle; anterior inner list small (relative to other species), set with few and short ridges. RV with inner list present, but weakly developed (not produced away from inner lamella); this valve with a weak indention at the antero-dorsal corner. Anterior and posterior calcified inner lamellae relatively narrow in both valves.
A1 (Fig. 1B) with first podomere with 2 subapical ventral and one medio-dorsal setae, all hirsute. Second podomere with small, but clear, medio-ventral Rome organ and minute dorso-apical seta. Third podomere with two apical setae, the ventral not reaching the edge of the terminal segment; the dorsal one reaching well beyond the edge of this segment. Fourth and fifth podomeres each with two dorsal and two ventral setae, the former almost twice as long as the latter. Sixth (penultimate) podomere with four long and one shorter setae. Terminal segment with one long aesthetasc Ya, a short, claw-like seta (reaching beyond Ya) and two long setae. The longest natatory setae 2-2.5 times the length of the last 5 segments combined.
A2 (Fig. 1D,N,T) with exopodite consisting of 2 short and 1 long seta, the latter reaching slightly beyond the tip of the first endopodal segment. Natatory setae short, mostly reaching halfway the penultimate segment, except for the first n.s., always the longest and mostly reaching the tip of the penultimate segment. The latter segment with 2 dorsal setae, 4 unequal ventral t-setae, 3 long subapical z-setae (not reaching beyond the tip of the endclaws), 2 long and one shorter claws (G1-G3) and two aesthetascs: y1 close to the t-setae and y2 near the insertion of the terminal segment. Terminal segment with one long GM and one short (Gm) claw, aesthetasc y3 fused with a seta (the seta longest) and one longer seta (g), the latter longer than Gm. All claws set with two rows of small

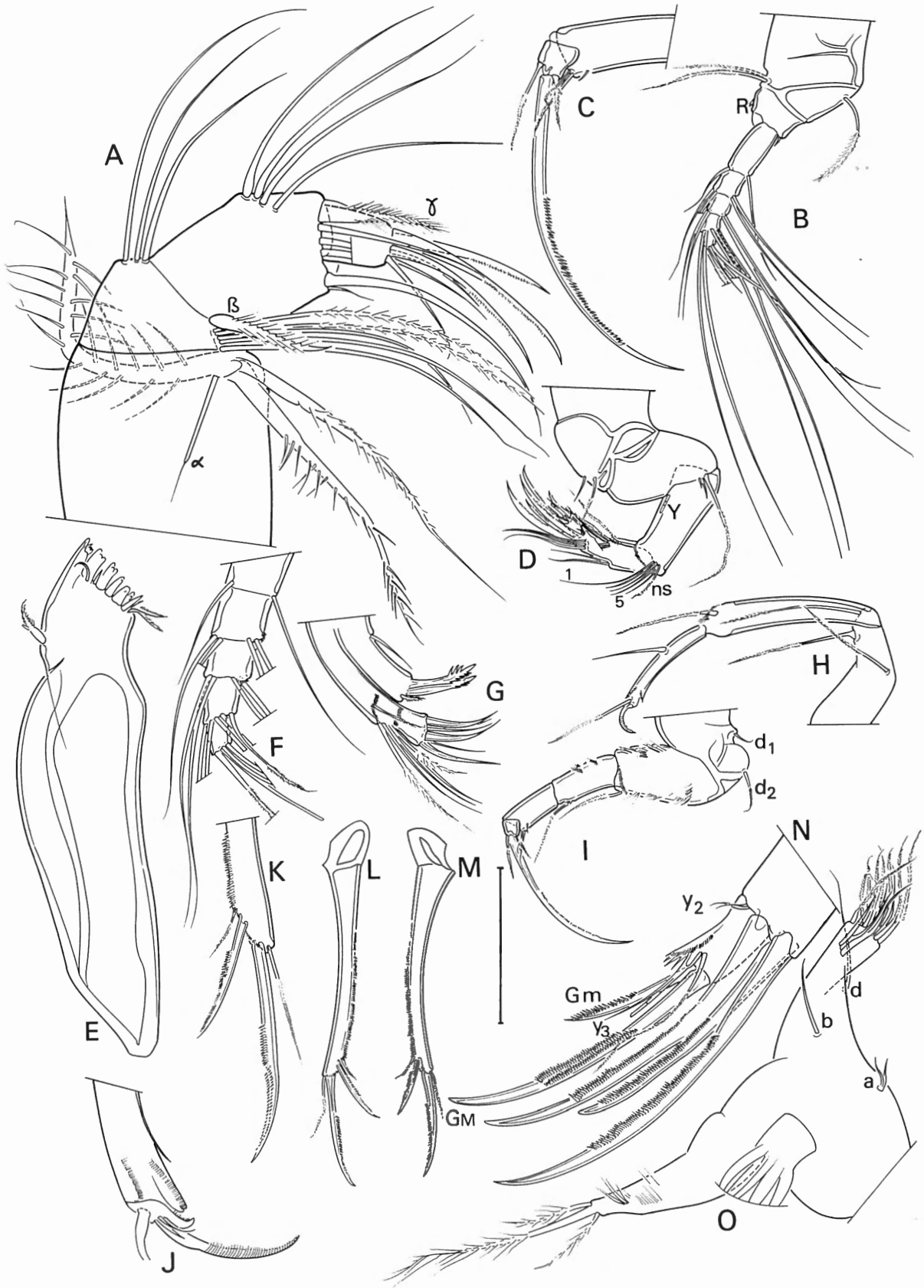

Fig. 1. – *Herpetocypris reptans* (female, Belgium).
A. *Md-palp (OC.1895)*. B. *A1 (OC.1895)*. C. *T1, detail of apical chaetotaxy (OC.1894)*. D. *A2 (OC.1895)*. E. *Md-coxa (OC.1895)*. F. *A1, detail of apical chaetotaxy (OC.1895)*. G. *Mx1, part of chaetotaxy (OC.1895)*. H. *T2 (OC.1895)*. I. *T1 (OC.1894)*. J. *T2, detail of apical chaetotaxy (W1004)*. K. *Fu, detail of apical chaetotaxy (OC.1894)*. L. *Fu (OC.1894)*. M. *Fu (OC.1894)*. N. *A2, detail of apical chaetotaxy (OC.1895)*. O. *Mx2 (OC.1895)*.
Scale: 100 µm for J; *102 µm for* A, N; *200 µm for* C, E, F, G, K, O; *420 µm for* B, D, H, I, L, M.

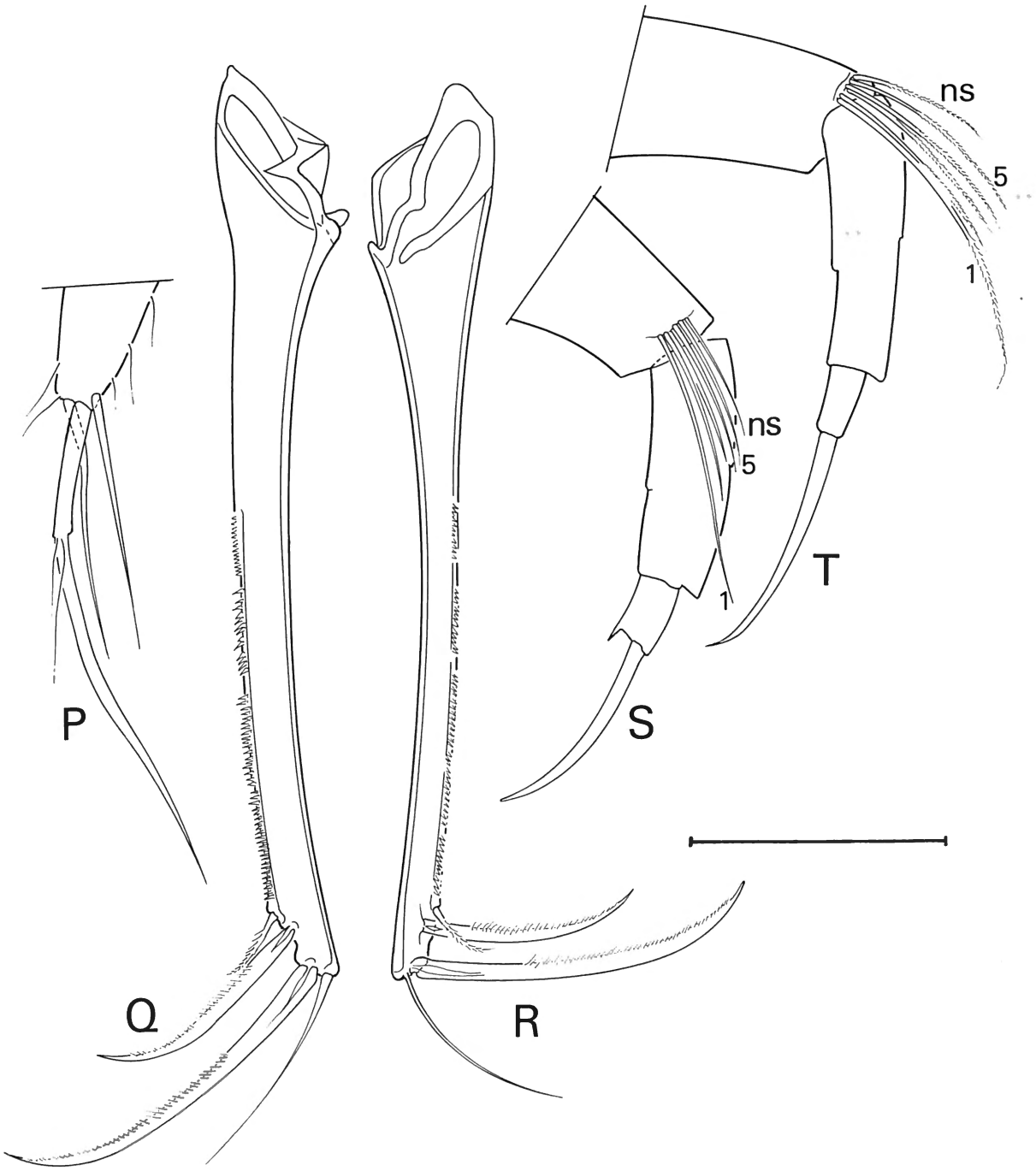

Fig. 1(bis). – *Herpetocypris reptans curvata* (P-S, female, type, Switzerland), *H. reptans reptans* (T, female, Belgium).
P. *Mx2-palp, distal part (MG139).* Q. *Fu (MG139).* R. *Fu (MG139).* S. *A2, showing length of natatory setae* (*MG139*).
T. *A2, showing length of natatory setae* (*MG139*).
Scale: 102 µm for P; *200 µm for* Q-T.

spines, the 3 longest claws smooth in their distal fifth. Md with coxa (Fig. 1E) without special features. Md-palp (Fig. 1A) of normal Cypridinid shape; alpha-seta narrow and smooth, abruptly tapering towards the distal part, both beta and gamma-setae stout and hirsute. First segment with respiratory plate (not drawn), 2 stout s-setae (with alpha-seta in the middle) and an additional long seta, normally smooth but here hirsute. Beta-bundle (bundle of setae surrounding beta-seta on second palp segment) consisting of 3 smooth and 2 hirsute setae, all long. Second segment further with 3 dorsal setae. Penultimate segment with 4 subequal subapical smooth setae, one long and one minute ventro-apical setae and 3 smooth and one hirsute (gamma) apical setae. Terminal segment with three claws and three setae.

Mx1 (Fig. 1G) with second palp segment spatulate, set with three stout claws and three setae; first palp segment with one medial and 5 subapical setae, two hirsute and three smooth. Third endite with 'Zahn-borsten' serrate. First and second endites and respiratory plate without special features.

Mx2 (Fig. 10) with two small a-setae, 1 smooth b- and

d-setae. Endite (?) with a separate group of 3 smooth setae between d-seta and 10 apical setae; palp with one long medial and two smaller (about half the length) lateral apical setae.T1 (Figs. 1C,I) with seta d2 slightly longer than d1; penultimate segment divided, endclaw slightly longer than length of three last segments combined.
T2 (Figs. 1H,J) a cleaning limb, as typical of the family.
Furcae (Figs. 1K-M) symmetrical, rami set with variable group of spines, proximal seta relatively long, reaching slightly beyond edge of ramus; distal seta longer than half the length of the distal claw.
Males unknown.

Measurements
New measurements: RV = 2.30 mm (2.18-2.6) (n = 6); LV = 2.39 mm (2.23- 2.74) (n = 7).
Measurements from literature: KAUFMANN (1900): L = 2.64 mm; H = 1.19 mm; W = 1 mm; KLIE (1938): L = 2.1-2.6 mm; ROME (1947a): L = 2.1-2.6 mm

Distribution
West and Central Europe.

Habitat
The species occurs in ponds and small lakes; as well as in slowly flowing waters.

Remarks
1. ROME (1947a) described a male of what he called *H. reptans*. Reinvestigation of the material used for this description, revealed that he was dealing with two species. At least some of the females he dealt with belonged to *H. reptans* s.s.. However, at least the male from Morocco belonged to *H. brevicaudata* (see below), because of the largely inferior size, the different furca and especially the fact that in the male, the 5th n.s. of the A2 is the longest, not the 1st as in *H. reptans*. It is here confirmed that all males of *Herpetocypris* thus far described (GAUTHIER 1928 a, b, PETKOVSKI 1964, and various new populations reported in the present paper) belong to *H. brevicaudata*; all other species are exclusively known from parthenogenetic populations.
2. LÜTTIG (1955) described a new subspecies of *H. reptans*, as *Erpetocypris reptans aulicae*, from Elze and distinguished it from the nominal subspecies on a number of valve characteristics (almost equally rounded anterior and posterior margin straightly convex RV, greatest height in the middle, valves slightly higher) but provided no figures. Because of this, the validity of this subspecies is difficult to interpret, while the size of this subspecies also falls well into the range of *H. reptans reptans*. Until illustrations can show that *H. reptans aulicae* is a valid and morphologically distinct subspecies, we here consider it a synonym of *H. reptans reptans*.

Differential diagnosis
Herpetocypris reptans is the largest species in the genus; it can furthermore be distinguished from its congeners by the morphology of the anterior part of the LV, the short n.s. on A2 of which the 1st is always the longest, and the relatively long proximal furcal seta.

Herpetocypris reptans curvata KAUFMANN, 1900
(Figs. 1(P-S),18(H,I))

1900 *Erpetocypris reptans* var *curvata,* KAUFMANN, 282, Pl. 16(4-5), Pl. 18(27).

Type locality
Mendriso, Switzerland.

Diagnosis
All diagnostic features in valves and soft parts as in *H. reptans reptans*, but smaller and with different valve shape: dorsal margin more rounded.

Measurements (after KAUFMANN 1900):
L = 2.3 mm, H = 1.1 mm, W: 0.8 mm.

Distribution
Known from its type locality only.

Remarks
The population from Mendriso conforms in all details of soft part anatomy (typical length and configuration of the natatory setae on the A2, length of proximal furcal seta, etc) with *H. reptans reptans*. However, the shape of the valves is very different and analysis of several populations of *H. reptans reptans* showed that variability in valve shape in the nominal subspecies is minimal. We here consider *curvata* a subspecies of *H. reptans*.

Herpetocypris brevicaudata KAUFMANN, 1900
(Figs. 2(C,D), 3-9, 17(A-I), 19, 20)

1900 *Herpetocypris brevicaudata* n.s. KAUFMANN: 132, Pl. 16 (6-7); Pl. 18 (28-31)
1928 partim male *Erpetocypris reptans* (BAIRD) sensu GAUTHIER, fig. A-M.
1932 *Herpetocypris ghigii* n.sp. MASI, pp. 213-218, fig. a-e.
1938 *Herpetocypris brevicaudata* KAUFMANN, KLIE: 126-127, fig. 422-425.
1947 *Herpetocypris lenta* n.sp. ROME: 4-8, fig. 2 (a-g)
1964 *Herpetocypris brevicaudata* KAUFMANN, PETKOVSKI: 24-27, fig. 56-60
1967 *Herpetocypris flumendosa* n.sp. ANICHINI: 17-22
1968 *Herpetocypris brevicaudata* KAUFMANN, SYWULA: 37-39, fig. 14 (a-b), 15

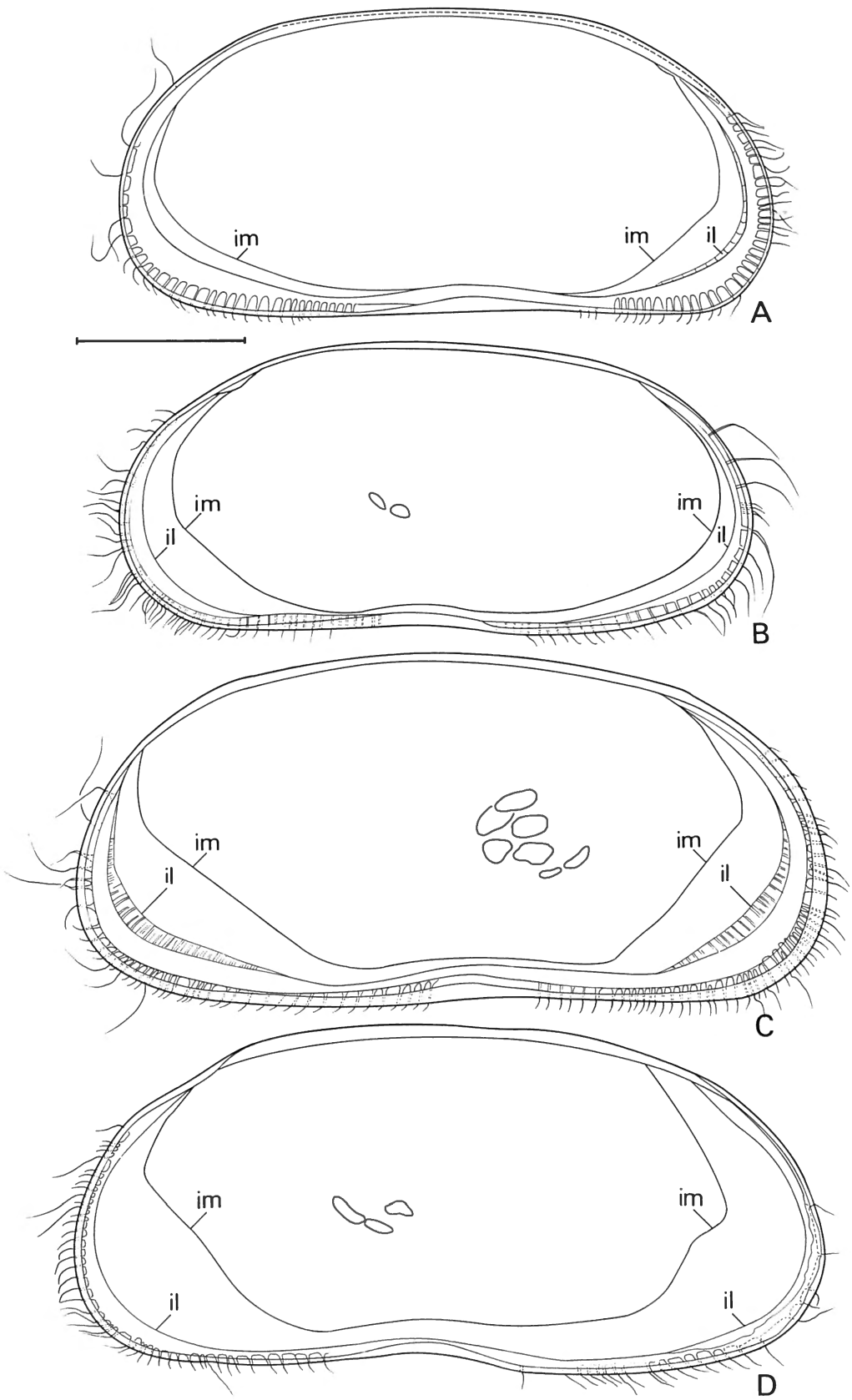

Fig. 2. – *Herpetocypris reptans reptans* (A-B, female, Belgium), *Herpetocypris brevicaudata* (C-D, female, Belgium).
A. *LV, internal view (W1027).* B. *RV, internal view (W1027).* C. *LV, internal view (OC.1954).* D. *RV, internal view (OC.1954).*
Scale: 410 µm for C, D; *960 µm for* A,B.

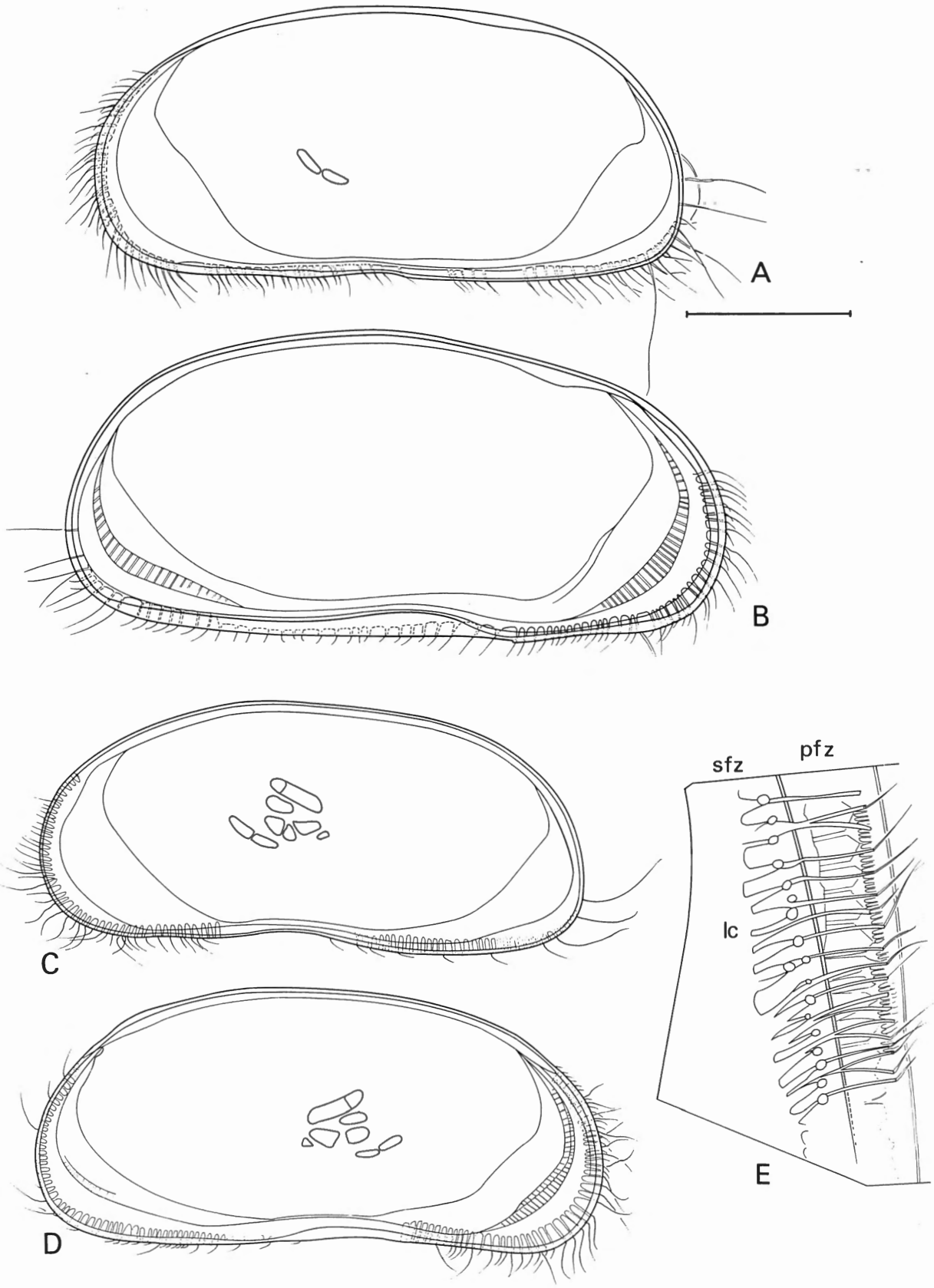

Fig. 3. – *Herpetocypris brevicaudata* (A-B, female, Algeria), *Herpetocypris brevicaudata* (C-D, male, Algeria).
A. *RV, internal view (OC.1960).* B. *LV, internal view (OC.1960).* C.*RV, internal view (OC.1991).* D. *LV, internal view (OC.1991).*E. *RV, detail of internal view (OC.1960).*
Scale: 102 µm for E; *410 µm for* A, B, C, D.

Fig. 4. – *Herpetocypris brevicaudata* (female, Belgium) A. *A1 (OC.1953)*. B. *A2 (OC.1955)*. C. *Md-palp (OC.1954)*. D. *A2, detail of apical chaetotaxy (OC.1955)*. E. *Mx1, part of chaetotaxy (OC.1955)*. F. *Md (OC.1955)*. G. *T2, detail of apical chaetotaxy (OC.1953)*. H. *Fu, detail of apical chaetotaxy (OC.1955)*. I. *T2 (OC.1953)*. J. *Mx2 (OC.1953)*. K. *Fu attachment (OC.1954)*. L. *T1 (OC.1955)*. M. *Fu (OC.1955)*. N. *Fu (OC.1955)*.
Scale: 110 µm for C, D, E, G, H, J; *156 µm for* A, B, F, I, K, L, M, N.

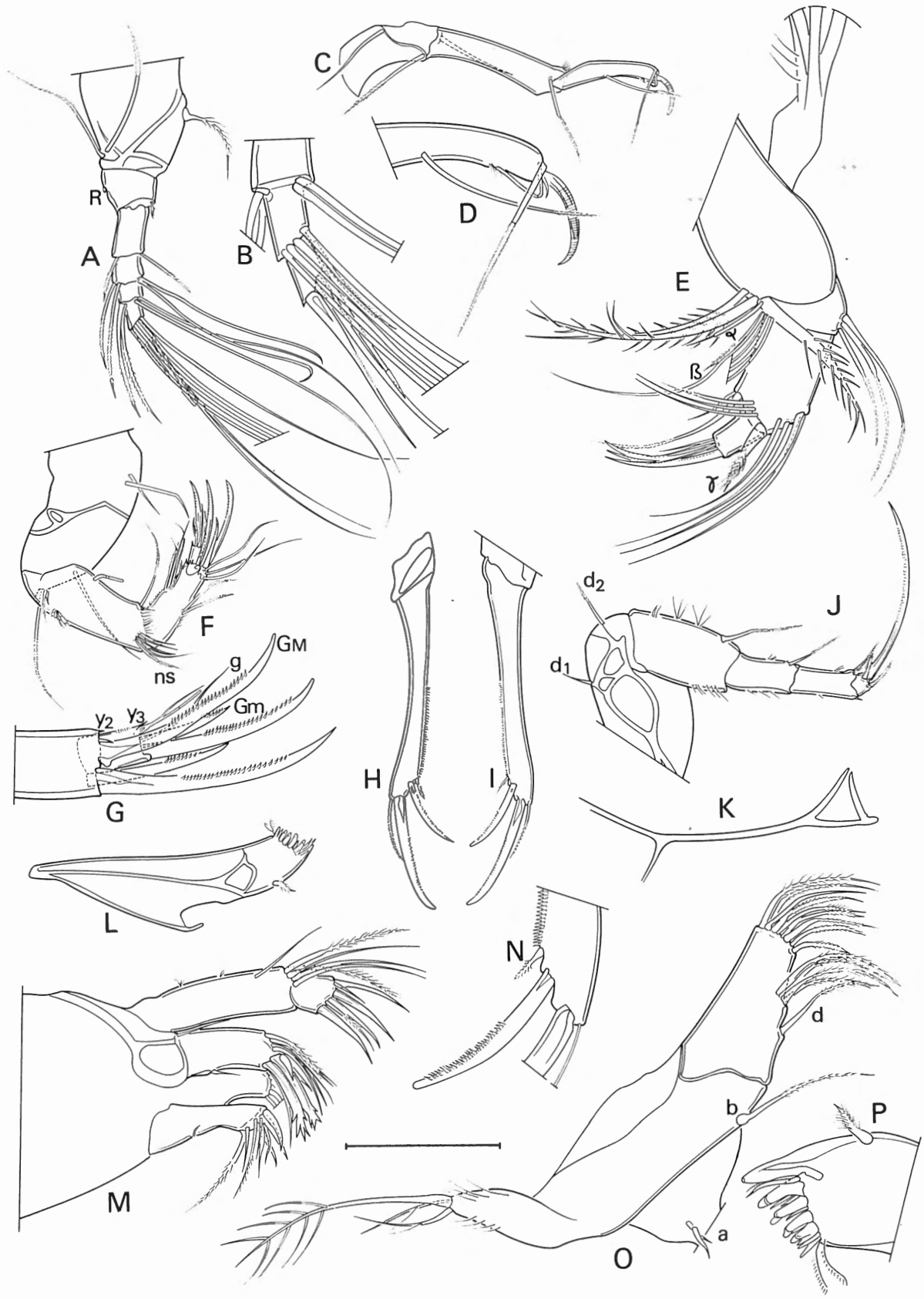

Fig. 5. – *Herpetocypris brevicaudata* (female, Algeria)
A. *A1 (OC.1990)*. B. *A1, detail of apical chaetotaxy (OC.1990)*. C. *T2 (OC.1990)*. D. *T2, detail of apical chaetotaxy (OC.1990)*. E. *Md-palp (OC.1990)*. F. *A2 (OC.1990)*.G. *A2 detail of apical chaetotaxy (OC.1990)*. H. *Fu (OC.1990)*.I. *Fu (OC.1990)*.J. *T1 (OC.1990)*. K. *Fu attachment (OC.1990)*. L. *Md (OC.1990)*. M. *Mx1 (OC.1990)*. *N. Fu, detail of apical chaetotaxy (OC.1990)*. O. *Mx2 (OC.1990)*. P. *Md, detail of apical chaetotaxy (OC.1990)*.
Scale: 100 µm for G; *110 µm for* B, D, E, M, N, O, P; *156 µm for* A, C, F, H, I, J, K, L.

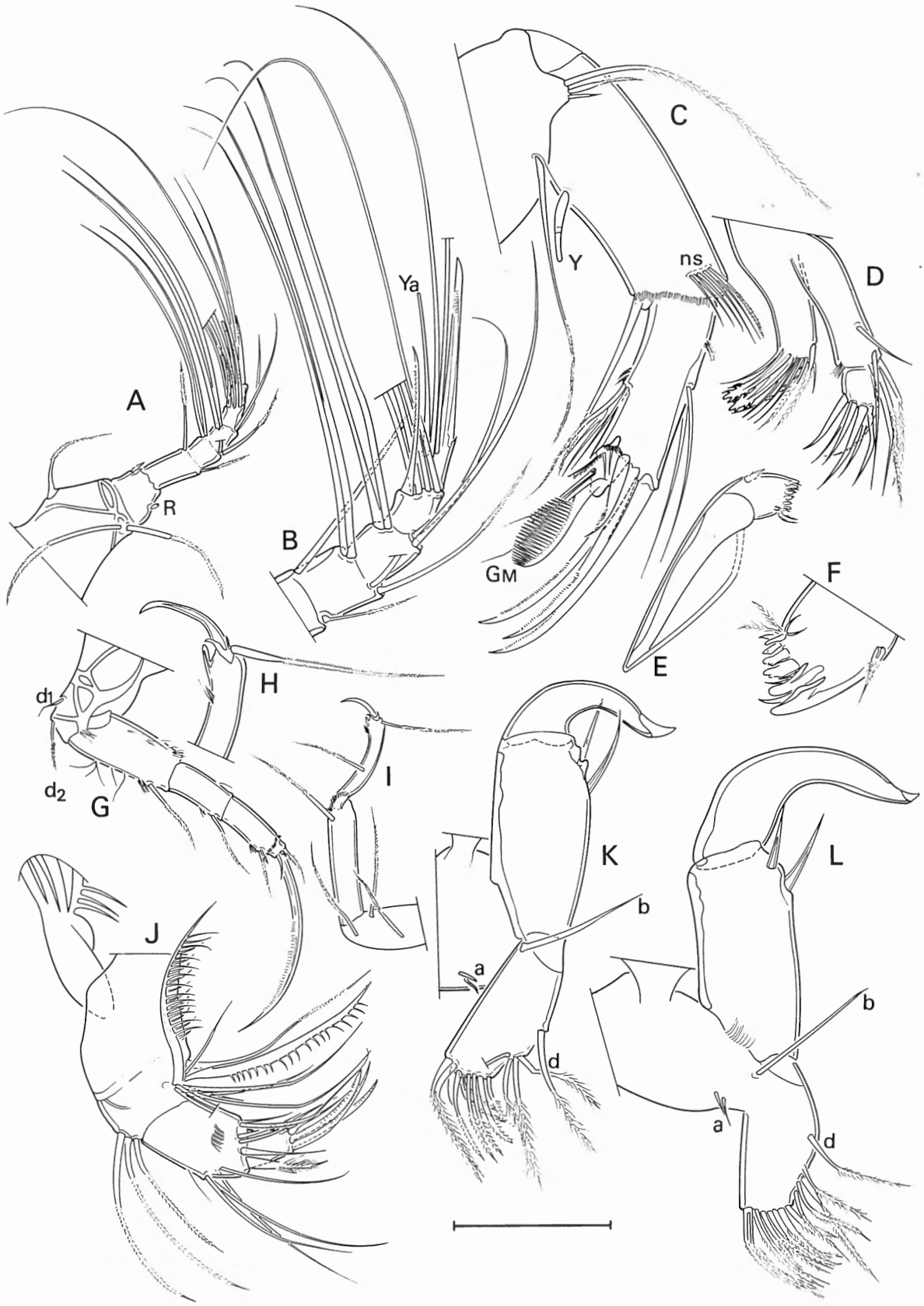

Fig. 6. – *Herpetocypris brevicaudata* (male, Algeria).
A. *A1 (OC.1991)*. B. *A1, detail of apical chaetotaxy (OC.1991)*.C. *A2 (OC.1991)*. D. *Mx1, part of chaetotaxy (OC.1991)*.E. *Md (OC.1991)*. F. *Md, detail of apical chaetotaxy (OC.1991)*. G. *T1 (OC.1991)*. H. *T2 detail of apical chaetotaxy (OC.1991)*. I. *T2 (OC.1991)*. J. *Md-palp (OC.1991)*. K. *left prehensile palp (OC.1991)*.L. *right prehensile palp (OC.1991)*. *Scale: 110 µm for* B,C, D, F, H, J, K, L; *156 µm for* A, E, G, I, J.

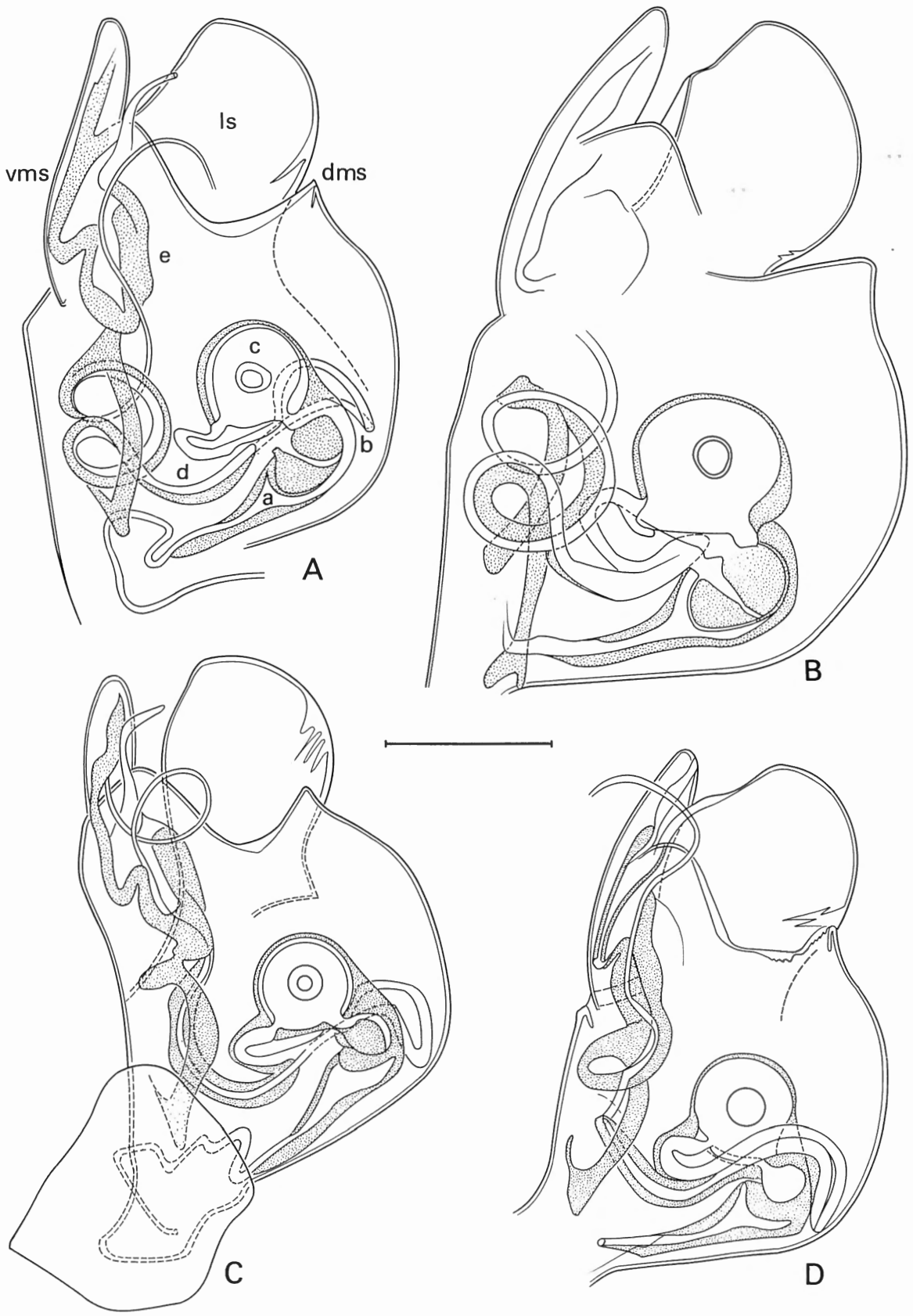

Fig. 7. – *Herpetocypris brevicaudata* (males), (A, Algeria; B, Spain; C-D, Algeria).
A. *Hemipenis (OC.1976)*. B. *Hemipenis (Fte. Pilar del Mono)*. C. *Hemipenis, erected position (OC.1980)*. D. *Hemipenis, erected position (OC.1980)*.
Scale: 100 µm for B; *110 µm for* A, C, D.

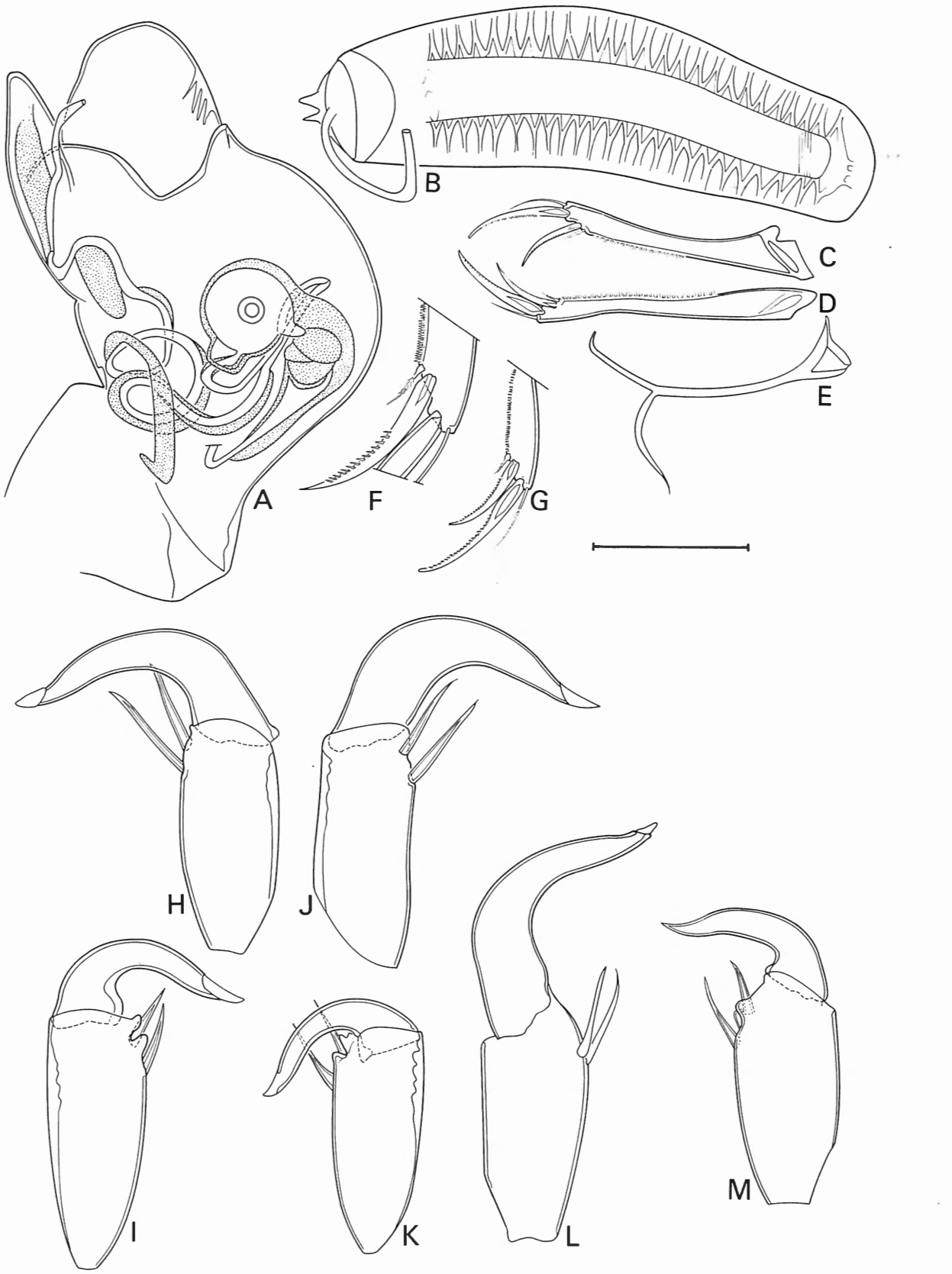

Fig. 8. – *Herpetocypris brevicaudata* (A-K, male, Algeria; L-M, male, Spain)
A. *Hemipenis (OC.1991).* B. *Zenker Organ (OC.1991).*C. *Fu (OC.1991).* D. *Fu (OC.1991).* E. *Fu attachment (OC.1991).* F. *Fu detail of apical chaetotaxy (OC.1991).* G. *Fu, detail of apical chaetotaxy (OC.1991).* H. *right prehensile palp (OC.1976).* I. *left prehensile palp (OC.1979).* J. *right prehensile palp (OC.1979).* K. *left prehensile palp (OC.1976).* L. *right prehensile palp (Fte. Pilar del Mono).* M. *left prehensile palp (Fte. Pilar del Mono).*
Scale: 70 µm for L, M; *110 µm for* A, B, F, H, I, J, K; *156 µm for* C, D, E, I, J, K, L; *200 µm for* G.

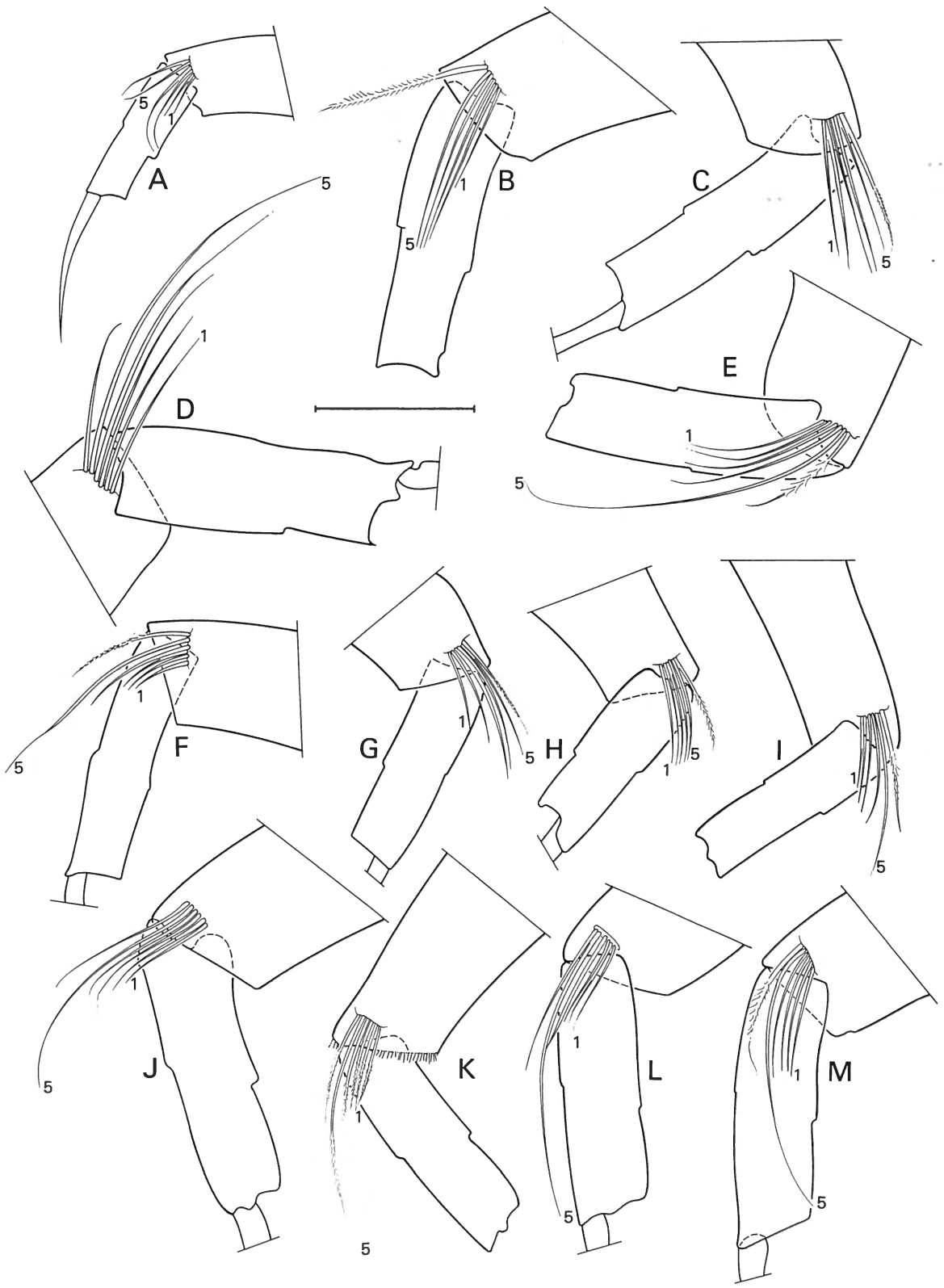

Fig. 9. – *Herpetocypris brevicaudata* (males and females). (A, C, E: Belgium, D: Spain, F-M: Algeria).
A. *A2, showing only length of natatory setae. (OC.1955).* B. *A2, showing only length of natatory setae. (OC.1954).* C. *A2, showing only length of natatory setae. (OC.1953).* D. *A2, showing only length of natatory setae. (MG040).* E. *A2, showing only length of natatory setae. (OC.1950).* F. *A2, showing only length of natatory setae. (OC.1994).* G. *A2, showing only length of natatory setae. (OC.1997).* H. *A2, showing only length of natatory setae. (OC.1996)* I. *A2, showing only length of natatory setae. (OC.1978).* J. *A2, showing only length of natatory setae. (OC.1967).* K. *A2, showing only length of natatory setae. (OC.1977).* L. *A2, showing only length of natatory setae. (OC.1961).* M. *A2, showing only length of natatory setae. (OC.1983).*
Scale: 110 µm for D, E, F, G, H, I, J, K, L; *102 µm for* B, C, M; *200 µm for* A.

1969 *Herpetocypris brevicaudata* KAUFMANN, NÜCHTERLEIN: 263-265
1975 *Herpetocypris brevicaudata* KAUFMANN, DIEBEL & PIETRZENIUK, Pl. 4 (7-8)
1982 *Herpetocypris brevicaudata* KAUFMANN, TETART: 165, fig. 119-126
1984 *Herpetocypris brevicaudata* KAUFMANN, DIEBEL & PIETRZENIUK, Pl. 4 (9-10)
1987 *Herpetocypris brevicaudata* KAUFMANN, MEISCH: 107
1992 *Herpetocypris brevicaudata* KAUFMANN, BALTANAS: 427-431, fig. 1, 4
1996 *Herpetocypris brevicaudata* KAUFMANN, BEYER & MEISCH: 29-34

Type locality
Bülach, Nidau and Mendriso, Switzerland.

Diagnosis
Small species, with well developed calcified inner lamellae; anterior inner list in LV larger, more produced and set with more ridges than in the preceding species. Anterior calcified inner lamella in LV between inner list and valve margin with an abrupt angle. N.s. on A2 variable, generally short (not reaching tip of penultimate segment), 5th n.s. nearly always the largest. Proximal furcal seta not reaching tip of ramus. Syngamic populations known from the western part of the Mediterranean area only.
(Remark: as no males are known in other species, male characteristics cannot be used to distinguish species within this genus).

Extended diagnosis

FEMALE

Variable, generally small species, with dorsal margin of valves either parallel or rounded; caudal margin mostly not evenly rounded, but passing into dorsal margin with a blunt angle. Calcified inner lamellae in both valves significantly wider than in the preceding species and anterior inner list in LV larger, more produced and set with more ridges than in the preceding species. Anterior calcified inner lamella in LV between inner list and valve margin with an abrupt angle.
Longest setae on A1 about twice the length of the 5 terminal segments combined.
A2 with n.s. short, all of variable length (see fig. 9 and discussion) but 5th n.s. always the longest, in some specimens not reaching the middle, in others reaching beyond the tip of the penultimate segment. Seta g on terminal segment reaching beyond claw Gm. Two latero-apical setae on Mx2 palp one third (or less) of the length of the medio-apical seta; this palp often folded, but not divided into segments.
Furca with wide rami, set with variable groups of spines (figs); proximal seta not reaching tip of ramus; distal seta reaching about halfway the larger endclaw.

MALE

Valves, A1, Md, Mx1, T1, T2 and furca as in the female.
A2 (Fig. 6C) with distal chaetotaxy of penultimate segment as typical of Cyprididae (MARTENS, 1987), i.e. with setae z2 changed into a small, z3 into a large claw, claw G3 reduced to a seta. Unlike most other Cyprididae, however, there is also sexual dimorphism in the chaetotaxy of the terminal segment: claw Gm reduced to a long seta; claw GM changed into a large, "comb"like structure with one row of large spines.
Right prehensile palp (Fig. 6L,8H,J,L) the largest, with 2 subequal subapical sensory organs on penultimate segment; terminal segment curved and elongated, tapering in its distal half; with one distal sensory organ.
Left prehensile palp (Figs. 6K, 8I,K,M) smaller, sensory organs on penultimate segment unequal (the distal one the shortest); terminal segment sickle-shaped, tapering from the basis onwards; with one distal sensory organ.
Hemipenis (Figs. 7A-D, 8A) with both lateral and distal shields somewhat variable. Distal part of medial shield prominent, subrectangular, but (possibly because of three-dimensional structure), with variable lateral margins when flattened in slide. Distal part of lateral shield with one small, pointed dorsal lobe and an elongated, finger-like ventral lobe. Internal anatomy: labyrinth with bladder-like part 'c' (typical of Herpetocypridinae); post-labyrinthal spermiduct with only one weak additional coil (several large additional coils possible in other genera and subfamilies); distal part of spermiduct nearly always positioned outside of the shields, along the finger-like ventral lobe, both in relaxed (Figs. 7A,B) and in erected (Figs. 7C,D) position.
Zenker organ (Fig. 8B) elongated, with c. 25 spinuous whorls (exact number variable).

Measurements

FEMALES

New measurements L=: RV = 1.62 mm (1.31-1.89) (n = 28); LV = 1.70 mm (1.37-1.97) (n = 31).
Measurements from literature: GAUTHIER (1928 a) (as *H. reptans*): L = 1.9-1.95 mm; LOWNDES (1931): L = 1.7 mm; H = 0.8 mm; T = 0.7 mm; KLIE (1938): L = 1.7-2.2 mm; ROME (1947 b) (as *H. lenta*): LV = 1.9 mm; SYWULA (1968): L = 1.76-1.81 mm; TETART (1982): L = 1.85-1.95 mm; MEISCH (1987): L = 1.8-1.92 mm; MASI (1932a) (as *H. ghigii*): L = 1.8 mm; ANICHINI (1968 a) (as *H. flumendosa*): L = 1.86 mm; H = 0.83 mm; W = 0.76 mm.

MALES

New measurements: RV = 1.42 mm (1.32-1.58) (n = 9); LV = 1.47 mm (1.36-1.66) (n = 9)
Measurements from literature: GAUTHIER (1928 a) (as *reptans*): L = 1.68 mm.

Habitat
Occurs in a variety of different climatological regions and habitats: in permanent streams, lakes, ponds, springs. Some of the North African localities could be temporary.

Distribution
Parthenogenetic populations are known throughout Europe; bisexual populations are reported from North Africa (Algeria) and Portugal, i.e. in the Western part of the Mediterranean area.

Remarks
1. Several forms of this species have in the past been described as separate species (see list of synonymies) and to assess whether or not the range of variability in this species was continuous (intra-specific) or disjunct (inter-(sub)specific) indeed constituted the major part of the present revision. Two major carapace shapes exist: larger, more elongated carapaces versus smaller, dorsally more rounded carapaces. The former occur more in the parthenogenetic populations of Western Europe, the latter occur more often in both the bisexual and parthenogenetic populations of the Mediterranean area. However, these forms cannot be allocated any taxonomic rank, because of the following reasons: (1) intermediate shapes occur, so that the above shapes must be seen as extremes of a variability range; (2) both extremes can occur in the same population, (3) both males and (presumed) bisexual females can occur in both shapes; (4) the observed variability in soft part morphology (length of A2 n.s., Mx2-palp) is independent from the carapace shape; (5) morphological variability in the copulatory module of males (A2, hemipenis, prehensile palps - DANIELOPOL *et al.* 1990) is independent of carapace shape.
2. Based on type materials, we here sink *H. ghigii* MASI and *H. lenta* ROME into the synonymy of *H. brevicaudata*. Of *H. flumendosa*, we have vainly tried to obtain type materials (as is also the case for the other species of ANICHINI). However, in this case the description of *H. flumendosa* was sufficient to place it within the range of variability observed in *H. brevicaudata*.

Differential diagnosis
The small size, the short n.s. on A2, with the 5th, not the 1st, being generally the largest, the relatively short proximal furcal seta and, around the Mediterranean, the presence of males, allow identification of this otherwise very variable species.

Herpetocypris mateusorum PAULO, 1969
(Figs. 10, 21(A-J))

1969 *Herpetocypris mateusorum*, n.sp. PAULO: 14-37, fig. 1 (a-b), 2-6, 7(a-c), 8-14, 15(a-b), 16-17
1992 *Herpetocypris mateusorum* (PAULO), BALTANAS 432, fig. 1, 6(a-b)

Type locality
Pool at Castelo do Queijo, near Porto, Portugal.

Abbreviated Diagnosis
Valves with rounded dorsal margin, RV with anterior inner list situated close to the valve margin, LV with anterior inner list prominent, but also situated more closely to valve margin than in other species; calcified inner lamellae in LV between inner list and valve margin with an abrupt angle.
Natatory setae on A2 (Fig. 10G) of intermediate length, n.s. 1-5 subequal and mostly reaching beyond tip of penultimate segment, but not reaching tips of endclaws.

Measurements
(from PAULO, 1969): L = 1.7 mm; H = 0.86 mm; W = 0.71.

Distribution
Endemic to the western part of the Iberian peninsula (Portugal, W. Spain).

Habitat
Small permanent lakes, lakelets and rivulets, fresh to slightly saline.

Remarks
There are several inaccuracies in the original description of this species (PAULO, 1969), which have caused confusion in the literature. Firstly, the drawing of the valve (PAULO 1969: fig. 1a) shows a much shorter and higher valve, rather atypical of the genus. Secondly, in the description, the 5th n.s. on the A2 is said to reach 1/3 of the length of Claw G1 ('atteint légèrement l'extrémité distal du premier tiers de la griffe terminale', p. 21), whereas fig. 3 (in PAULO 1969) shows that this n.s. barely reaches the tip of the penultimate segment. A visit to the Museum of Natural History in Porto by the senior author has produced a few specimens of what is supposedly the type material of *H. mateusorum*, although the tubes were not labelled as such. These specimens (kindly donated by the staff of the Porto-museum to the KBIN collection - see appendix) conform to most illustrations in PAULO (1969). The valves have the rounded dorsal margin, but are more elongated than in PAULO's illustration, and are thus less atypical of *Herpetocypris*. New collections around Porto have also yielded material of the same species, which we here consider to be *H. mateusorum*.

Differential diagnosis
The rounded valves, the position of the il on the RV and the intermediate length of the A2 n.s. differentiate this species from its congeners.

Fig. 10. – *Herpetocypris mateusorum* (female, Portugal).
A. *Md-palp (OC.1942)*. B. *Mx1, part of chaetotaxy (OC.1943)*. C. *T1 (OC.1943)*. D.*T2 (OC.1943)*. E. *A1 (OC.1943)*. F. *A2, detail of apical chaetotaxy (OC.1942)*. G. *A2 (OC.1942)*.H. *Fu (OC.1941)*. I. *Fu (OC.1942)*. J. *Mx2 (OC.1942)*. K. *Md, detail of apical chaetotaxy (OC.1943)*.
Scale: 102 µm for A, B, F, G, J; *200 µm for* D, H, I, K; *420 µm for* C,E.

Herpetocypris ehringdorfensis DIEBEL & PIETRZENIUK, 1975 (Figs. 21(K-M))

1975 *Herpetocypris ehringdorfensis* n.sp., DIEBEL & WOLFSCHLÄGER, 114-115. Fig. 21

Type locality
Ehringdorf, near Weimar (Germany) (Lower Pleistocene)

Abbreviated Diagnosis
Medium-sized species, with rounded dorsal margin, but with postero-dorsal part of LV higher than in the preceding species; i.l. of LV not as prominent as in most species. RV with anterior i.l. situated further inward from valve margin than in the preceding species.
Soft part morphology unknown.

Distribution
Known from its type locality only.

Remarks
This taxon cannot be placed in any of the Recent species, and we thus retain it as valid. Based on valve morphology only, it seems to take an intermediate position between *H. mateusorum* (shape, size) and *H. intermedia* (marginal valve anatomy).

Herpetocypris intermedia KAUFMANN, 1900 (Figs. 11(F-J), 17(O), 22)

1900 *Herpetocypris intermedia,* n.sp. KAUFMANN: 132, Pl. 16 (8-9), Pl. 21 (1-4)
1905 non *Cypris intermedia* var *latialis* MASI (= *Herpetocypris helenae*)
1931 *Herpetocypris intermedia,* LOWNDES: 83-87, fig. 1-23
?1968 *Herpetocypris andegavensis* n.sp. ANICHINI, 587-591, figs. 1-17

Type locality
Mendriso, Switzerland.

Abbreviated Diagnosis
Small to intermediately sized species, with relatively high and smoothly rounded dorsal margins; i.l. on LV prominent, large and ribbed; RV with anterior i.l. situated well inward from valve margin, but posterior i.l. relatively close to valve margin. N.s. on A1 2.5-3 times the length of 5 terminal segments combined. N.s. on A2 reaching distal half of claws. Mx2 palp with latero-apical setae less than half the length of the middle seta. Ratio of Mx2 palp-setae: sl/L = 0.31 (0.24-0.39); ss/L = 0.39 (0.39-0.40) (n = 2).

Measurements
New measurements: RV = 1.81 mm (1.81-1.82) (n = 2); LV = 1.89 mm (1.84-1.95) (n = 2).
Measurements from literature: KAUFMANN (1900): L = 2.01 mm; H = 0.92 mm; W = 0.79 mm; LOWNDES (1931): L = 1.9 mm; H = 0.84 mm; T = 0.7 mm; KLIE (1938): L = 1.7-2.2 mm.

Distribution
Reported from most of Europe, although in few localities.

Habitat
In large pools on swampy ground (LOWNDES, 1931).

Remarks
Based on the description of *H. andegavensis* ANICHINI, the synonymy of this species with *H. intermedia* is here confirmed.

Differential diagnosis
The medium-long n.s. setae on the A2 differentiate *H. intermedia* from *H. reptans*, *H. brevicaudata* and, to a lesser degree, from *H. mateusorum*. From the latter species, *H. intermedia* differs in the position of the anterior i.l. of the RV and in the shape of the valve (less rounded dorsal margin). *Herpetocypris intermedia* has different valves than *H. chevreuxi*, which generally also has longer n.s. on both A1 and A2. *Herpetocypris helenae* has more elongated valves, with more inwardly displaced posterior i.l. on LV; longer n.s. on A2 and longer latero-apical setae on the Mx2-palp.

Herpetocypris chevreuxi (SARS, 1889) (Figs. 11(A-E), 12, 13, 17(J-L), 23)

1889 *Stenocypris chevreuxi* SARS n.sp.: 3-27, Pl. 1-2
1938 *Herpetocypris chevreuxi* (SARS), KLIE: 127-128, fig. 426-428
1954 *Herpetocypris agilis* n.sp. ROME 26-31, fig. 7
1966 *Herpetocypris chevreuxi* (SARS), FOX: 34-36, fig. 4
1968 *Herpetocypris scoininosa* n.sp. ANICHINI, 83-88, Table 6
1982 *Herpetocypris chevreuxi* (SARS), TETART: 164-166, fig. 104-118
1987 *Herpetocyprys chevreuxi* (SARS), MEISCH: 108
1992 *Herpetocypris chevreuxi* (SARS), BALTANAS: 432, fig. 1
1995 *Herpetocypris chevreuxi* (SARS) MEISCH, et al.: 285
1996 *Herpetocypris chevreuxi* (SARS), BEYER & MEISCH, 29-34 (No illustr.)

Type locality
Swamp in Bon Kamera (Kharezas), Bona, Algeria.

Abbreviated Diagnosis
A large species, with widely inwardly situated anterior i.l. on LV. Postero-caudal part of both valves not produced.

Fig. 11. – *Herpetocypris chevreuxi* type (female, Algeria) (A-E) and *Herpetocypris intermedia* (Switzerland) *(F-J).*
A. *A1 (MG 128).* B. *A2, showing only length of natatory setae.(MG128).* C. *palp of Mx2 (MG128).* D. *Fu (MG128).* E. *Fu (MG128).* F. *A1 (MG140).* G. *A2, showing only length of natatory setae.(MG140).* H. *palp of Mx2 (MG140).* I. *Fu (MG140).* J. *Fu (MG140).*
Scale: 200 µm for A-J.

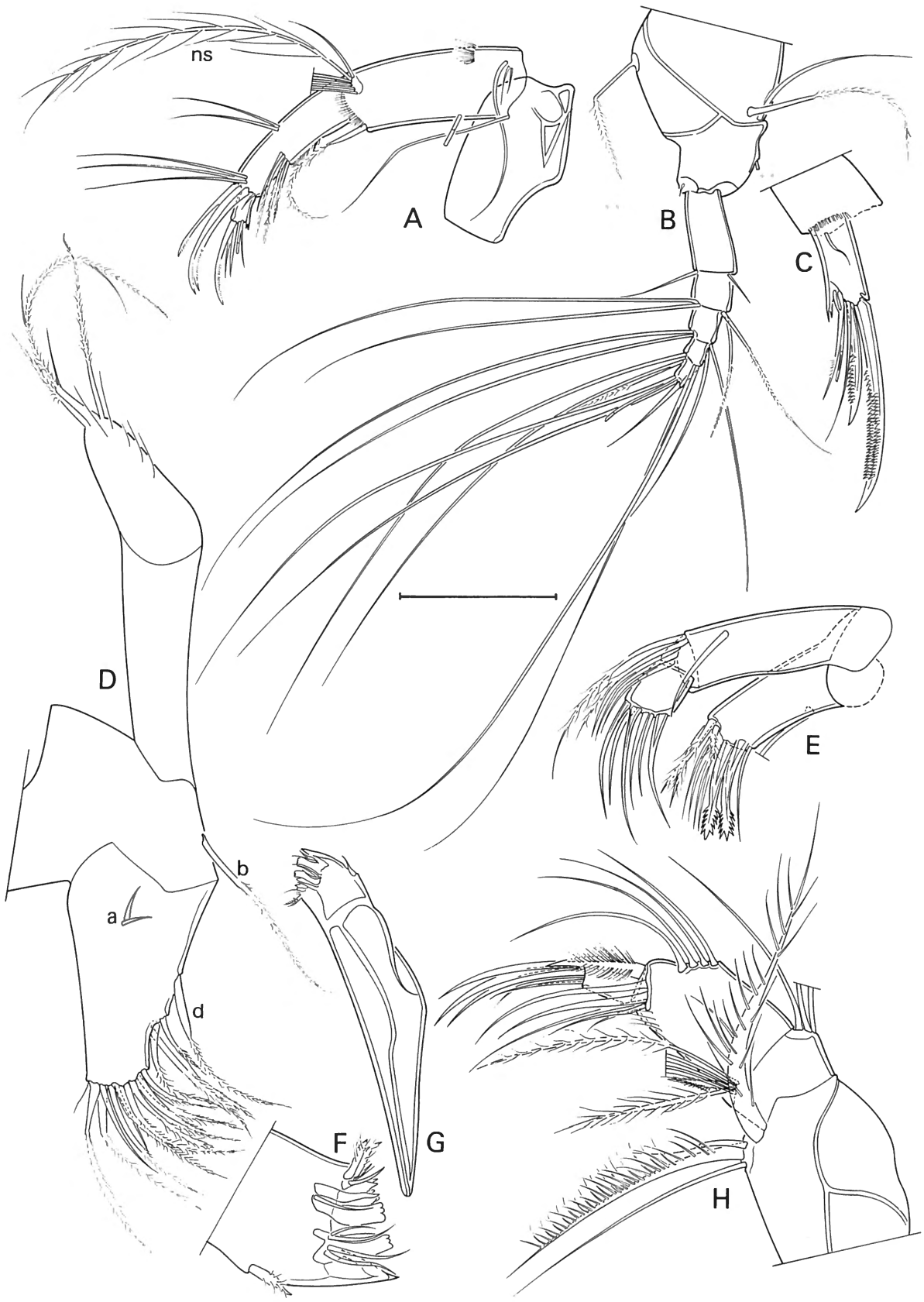

Fig. 12. – *Herpetocypris chevreuxi* (female, Belgium)
A. *A2 (OC.1936)*. B. *A1 (OC.1936)*. C. *A2, detail of apical chaetotaxy (OC.1936)*. D. *Mx2 (OC.1935)*. E. *Mx1, part of chaetotaxy (OC.1938)*. F. *Md, detail of apical chaetotaxy (OC.1939)*. G. *Md (OC.1939)*. H. *Md-palp (OC.1935)*. *Scale: 100 µm for* C; *110 µm for* D, E, F, H; *156 µm for* A, B, G.

Fig. 13. – *Herpetocypris chevreuxi* (female, Belgium).
A. *Fu (OC.1936)*. B. *Fu (OC.1936)*. C. *T2 (OC.1936)*. D. *T2 detail of apical chaetotaxy (OC.1936)*. E. *Fu attachment (OC.1937)*. F. *T1 (OC.1936)*. G. *A2, showing only length of natatory setae. (OC.1937)*. H. *A2, showing only length of natatory setae.(OC.1935)*. I. *Md-palp, showing alpha, beta and gamma-setae (OC.1935)*. J. *Fu, detail of apical chaetotaxy (OC.1936)*. K. *Fu, detail of apical chaetotaxy (OC.1935)*. L. *A2, showing only length of natatory setae.(OC.1939)*. M. *A2, showing only length of natatory setae.(OC.1938)*. N. *palp of Mx2 (OC.1938)*. O. *palp of Mx2 (OC.1939)*. P. *palp of Mx2 (OC.1936)*. Q. *palp of Mx2 (OC.1937)*.
Scale: 102 µm for K; *110 µm for* D, H, I, J, N, O, P, Q; *156 µm for* A, B, C, E, F, G, L, M.

Anterior i.l. on RV weakly developed, but present. N.s. on A1 very long, more than 3 times the length of 5 terminal segments combined. N.s. on A2 reaching to or beyond tips of claws. Largest of the latero-apical setae on Mx2-palp less than or half the length of the medio-apical seta; Ratio of Mx2 palp-setae: sl/L = 0.37 (0.26-0.58); ss/L = 0.48 (0.34-0.64) (n = 10). Furcae slender and with unique type of spines on ramus (not triangular as in other species, but long and with parallel sides).

Measurements
New measurements: RV = 2.13 mm (2.05-2.21) (n = 8); LV = 2.23 mm (2.18-2.29) (n = 7).
Measurements from literature: SARS (1889): L = 2.4 mm; KLIE (1938): L = 2.4 mm; MEISCH (1987): L = 2.6-2.8 mm; MEISCH *et al.* (1995): L = 1.95-2.35 mm.

Distribution
Thus far reported from most of Europe, although some populations identified as *H. chevreuxi* should doubtlessly be allocated to *H. helenae*.

Habitat
In ponds, lakes and slowly flowing streams, mostly (all?) permanent, fresh or slightly saline, as in coastal ponds near estuaries.

Remarks
1. A population from Belgium (De Panne - see appendix) has aberrant features in valve morphology (Figs. 23(G-I, P-R)): the valves are posteriorly highly arched and have because of this a dorsal margin sloping towards the front. Additionally, the inner list of the RV is nearly completely reduced. However, soft part morphology is identical to that of *H. chevreuxi* s.s. and the differences in valve morphology are in all probability due to decalcification of the material.
2. Based on type material, we confirm the synonymy of *H. agilis* ROME with the present species. Based on the (admittedly incomplete) description of *H. scoininosa* ANICHINI, we confirm the synonymy of this species with *H. chevreuxi*.

Differential diagnosis
The long n.s. of the A1 and the weakly produced postero-ventral corners of both valves are unique to this species, which can also be separated from *H. reptans* and *H. brevicaudata* (and to a lesser degree also from *H. mateusorum* and *H. intermedia)* by the long n.s. on the A2. The species is further separated from *H. mateusorum* by the position of the anterior i.l. on the RV. *Herpetocypris helenae* has valves with a more produced postero-ventral corner, relatively longer latero-apical setae on the Mx2-palp and shorter n.s. on the A1.

Herpetocypris helenae G.W. MÜLLER, 1908
(Figs. 14-16, 17(M,N), 24)

1905 *Cypris intermedia* var *latialis* MASI (unused senior synonym)
1908 *Erpetocypris helenae* n. sp., G.W. MÜLLER: 169, fig. 1-9
1932 *Herpetocypris palpiger* n.sp. LOWNDES: 155-201, fig. 1-4
1954 *Herpetocypris caerulea* n.sp. ROME: 21-25, fig. 6
1968 *Herpetocypris puteolina* n.sp. ANICHINI: 78-83, Table 5
1977 *Herpetocypris helenae* (MÜLLER), MCKENZIE: 445-446
1993 *Herpetocypris* cf. *helenae* (MÜLLER), BALTANAS & GARCIA-AVILES: 23-228, fig. 2(A-B), 3, 4(A-E), 5(A-E), 6(B-D)

Type locality
Island of St Helena.

Abbreviated Diagnosis
Elongated species, with straight dorsal margins, postero-caudal corners in both valves well produced. RV with posterior inner list blunt. N.s. on A1 shorter than in the preceding species (2-2.5 times the length of 5 last segments combined). N.s. of A2 reaching to or slightly beyond tips of claws. Largest of the latero-apical setae on Mx2-palp 2/3-3/4 of the length of medial one. Ratio of Mx2 palp-setae: sl/L = 0.54 (0.4-0.7); ss/L = 0.63 (0.42-0.82) (n = 12).

Measurements
New measurements: RV = 1.83 mm (1.6-2.16) (n = 14); LV = 1.92 mm (1.73-2.21) (n = 14).
Measurements from literature: G.W. MÜLLER (1908): L = 1.85-1.95 mm; BALTANAS & GARCIA-AVILES (1993): L = 1.87 mm.

Distribution
The species has thus far been found in most of Europe, as well as in North (including the Levant) and southern Africa.

Habitat
In lakes, ponds and slow flowing rivulets; both in vegetated belts and in the bare littoral of man-made lakes.

Remarks
Based on the re-examination of type-materials, *Herpetocypris caerulea* (Figs. 24 G,H,P), *H. palpiger* (Figs. 24 I,J) and *H. intermedia latialis* (Figs. 24 K,L) are placed into the synonymy of *H. helenae*. Based on the, admittedly incomplete, original description, we also sink *H. puteolina* into the synonymy of *H. helenae*.

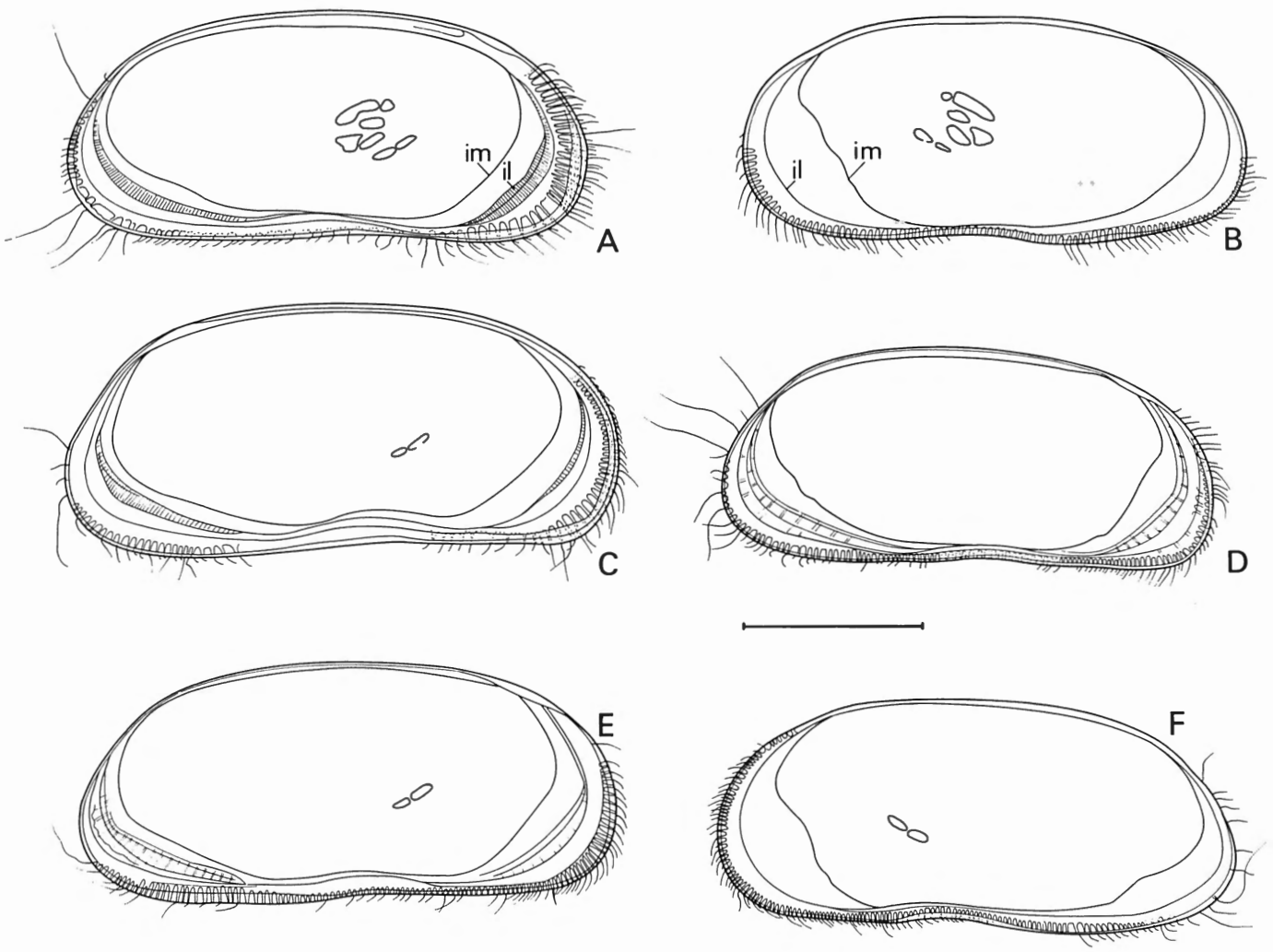

Fig. 14. – *Herpetocypris helenae* (A-B) (female, South Africa), *Herpetocypris caerulea* (C, female, type, Belgium), *Herpetocypris palpiger* (D, type, female, England), *Herpetocypris intermedia* var. *latialis* (E-F, type, female, Italy).
A. *LV, internal view (OC.1905).* B. *RV, internal view (OC.1905).* C. *LV, internal view (W1129).* D. *LV, internal view (MG130).* E. *LV, internal view (MG129).* F. *RV, internal view (MG129).*
Scale: 960 µm for A, B, C, D; *410 µm for* E, F.

Differential diagnosis
The species is closely related to both *H. chevreuxi* and *H. intermedia*. It differs from both in the shape of the valves, length of the n.s. of the A1 and A2 and relative length of setae on Mx2-palp.

Synonymies

The following is a survey of the European species of *Herpetocypris* and their synonyms.

Herpetocypris reptans (BAIRD, 1835)
Herpetocypris reptans reptans (BAIRD, 1835)
Herpetocypris reptans curvata KAUFMANN, 1900

Herpetocypris brevicaudata KAUFMANN, 1900
syn. *Herpetocypris ghigii* MASI, 1932
syn. *Herpetocypris lenta* ROME, 1947
syn. *Herpetocypris flumendosa* ANICHINI, 1967

Herpetocypris mateusorum PAULO, 1969

Herpetocypris ehringdorfensis DIEBEL & PIETRZENIUK, 1975

Herpetocypris intermedia KAUFMANN, 1900
? syn. *Herpetocypris andegavensis* ANICHINI, 1968

Herpetocypris chevreuxi (SARS, 1989)
syn. *Herpetocypris agilis* ROME, 1954
syn. *Herpetocypris scoininosa* ANICHINI, 1968

Herpetocypris helenae G.W. MÜLLER, 1908
syn. *Herpetocypris palpiger* LOWNDES, 1932
syn. *Herpetocypris caerulea* ROME, 1954
syn. *Herpetocypris puteolina* ANICHINI, 1968
syn. *Cypris intermedia latialis* MASI, 1905

Fig. 15. – *Herpetocypris helenae* (female, South Africa).
A. *A1 (OC.1905)*. B. *Mx1 (OC.1909)*. C. *A2 (OC.1906)*. D. *A1, detail of apical chaetotaxy (OC.1905)*. E. *A2, detail of apical chaetotaxy (OC.1906)*. F. *Mx2 (OC.1899)*. G. *Md-palp (OC.1905)*. H. *Md (OC.1905)*. I. *Md, detail of apical chaetotaxy (OC.1899)*.
Scale: 110 µm for B, D, E, F, G, I; *156 µm for* A, C, H.

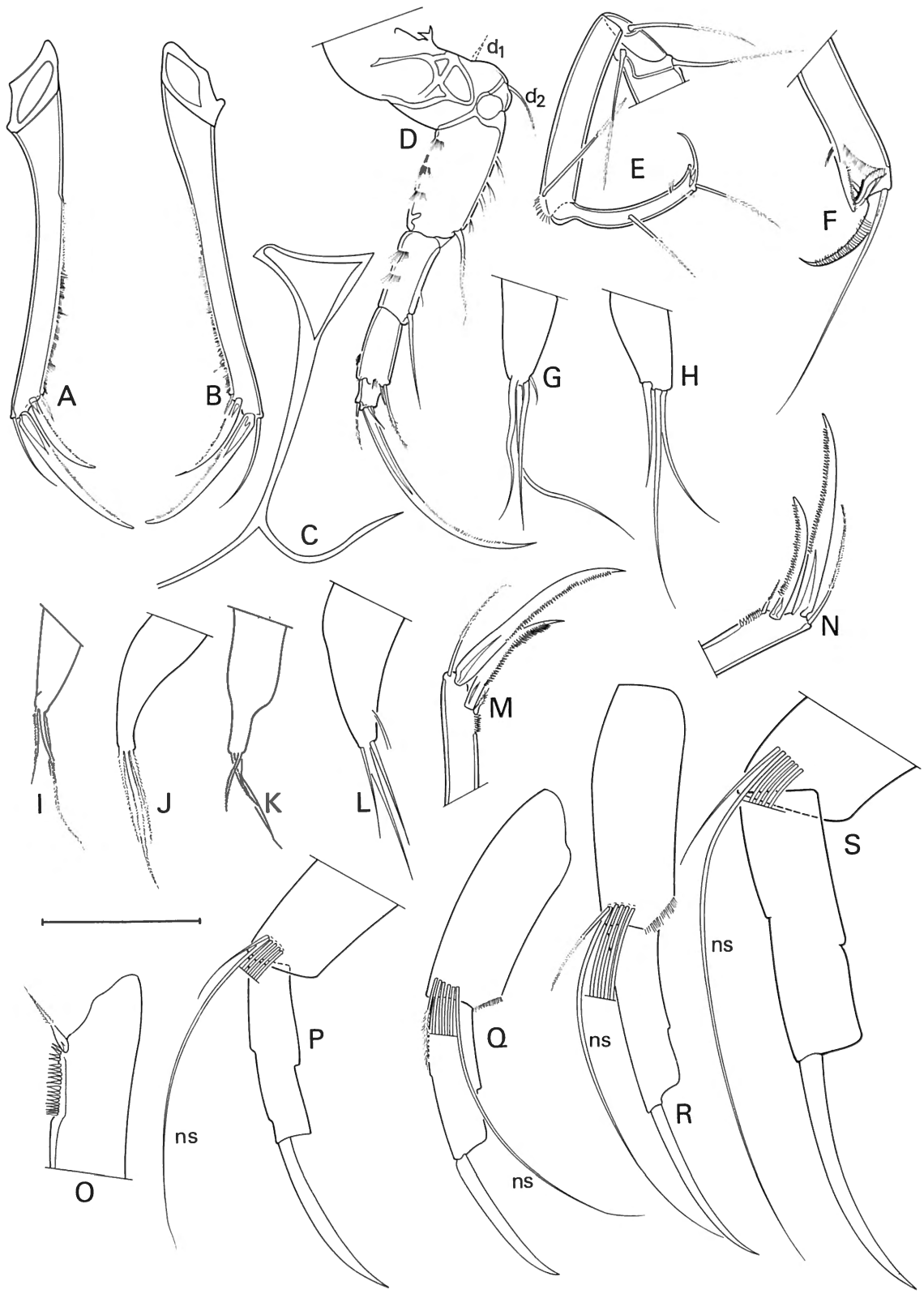

Fig. 16. – *Herpetocypris helenae* (A-H, M-O:female, South Africa) (I, R: England) (J-K, P-Q: Spain) (L, S: Algeria).
A. *Fu (OC.1907)*. B. *Fu (OC.1907)*.C. *Fu attachment (OC.1901)*.D. *T1 (OC.1899)*. E. *T2 (OC.1904)*. F. *T2 detail of apical chaetotaxy (OC.1901)*. G. *palp of Mx2 (OC.1909)*. H. *palp of Mx2 (OC.1908)*. I. *palp of Mx2 (GR001)*. J. *palp of Mx2 (GR004)*. K. *palp of Mx2 (OC.1922)*. L. *palp of Mx2 (OC.1918)*. M. *Fu detail of apical chaetotaxy (OC.1907)*. N. *Fu detail of apical chaetotaxy (OC.1907)*. *O. Fu, detail showing only the teeth (OC.1907)*.P. *A2, showing only length of natatory setae.(OC.1922)*. Q. *A2, showing only length of natatory setae.(OC.1921)*. R. *A2, showing only length of natatory setae.(GR001)*. S. *A2, showing only length of natatory setae.(OC.1918)*.
Scale: 102 µm for O; *110 µm for* F, G, H, L, S; *200 µm for* I, J, K, M, N, P, Q, R; *156 µm for* A, B, C, D, E.

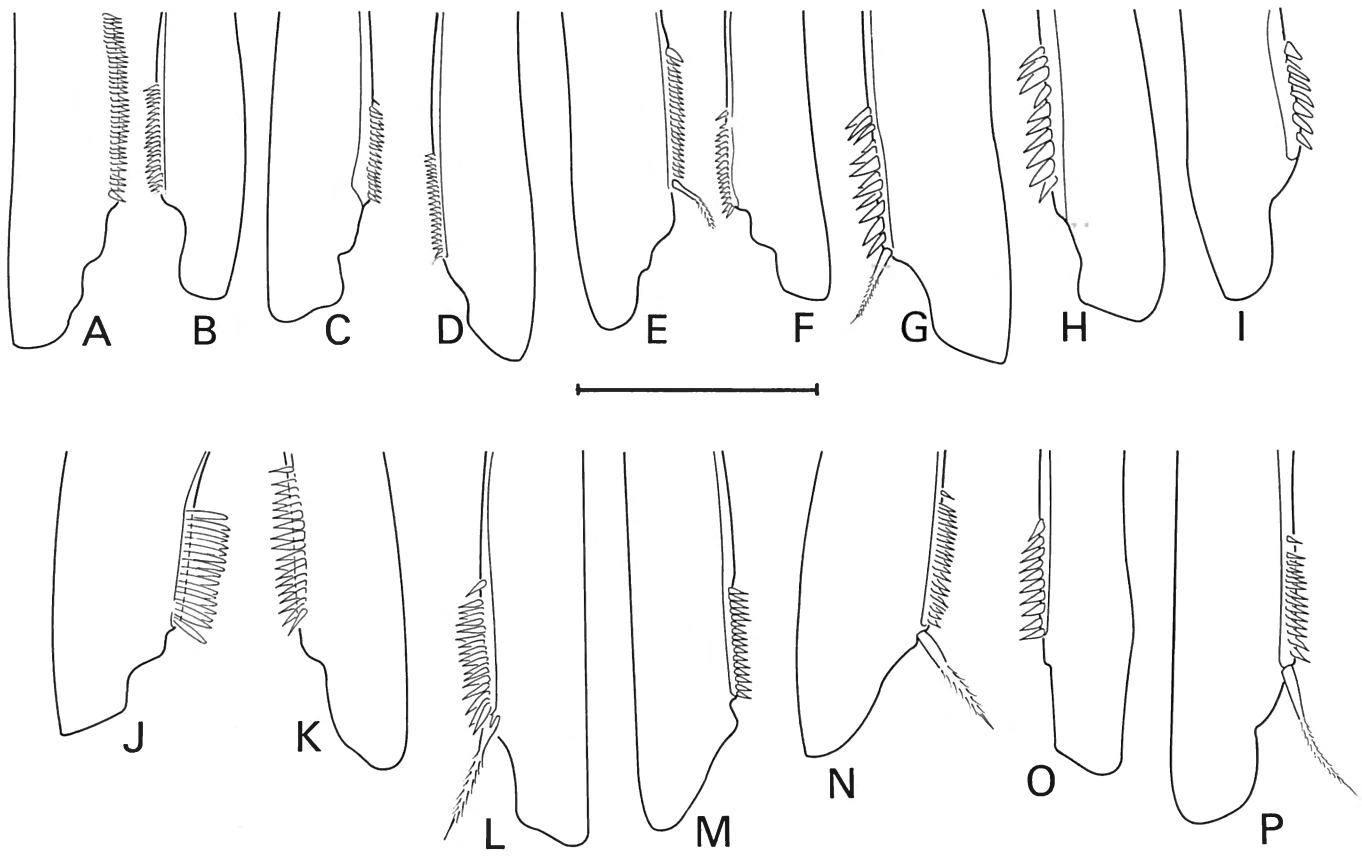

Fig. 17. – *Herpetocypris brevicaudata* (A-F: Algeria; G: Spain. H-I: Belgium). *Herpetocypris chevreuxi* (J-L,Belgium), *Herpetocypris helenae* (M: Algeria; N: Israel), *Herpetocypris intermedia* (O: Algeria), *Herpetocypris reptans* (P: Belgium).
A. *Fu, detail of apical chaetotaxy showing the last spines (OC.1960).* B. *Fu, detail of apical chaetotaxy showing the last spines (OC.1978).* C. *Fu, detail of apical chaetotaxy showing the last spines (OC.1990).* D. *Fu, detail of apical chaetotaxy showing the last spines (OC.1991 male).* E. *Fu, detail of apical chaetotaxy showing the last spines (OC.1989).* F. *Fu, detail of apical chaetotaxy showing the last spines (OC.1976,male).* G. *Fu, detail of apical chaetotaxy showing the last spines (MG040).* H. *Fu, detail of apical chaetotaxy showing the last spines (OC.1954).* I. *Fu, detail of apical chaetotaxy showing the last spines (OC.1955).* J. *Fu, detail of apical chaetotaxy showing the last spines (TYPE).* K. *Fu, detail of apical chaetotaxy showing the last spines (OC.1934).* L. *Fu, detail of apical chaetotaxy showing the last spines (OC.1923).* M. *Fu, detail of apical chaetotaxy showing the last spines (OC.1918).* N. *Fu, detail of apical chaetotaxy showing the last spines (OC.1920).* O. *Fu, detail of apical chaetotaxy showing the last spines (OC.1988).* P. *Fu, detail of apical chaetotaxy showing the last spines (OC.1894).*
Scale: 102 µm for A-P.

Discussion

MORPHOLOGY: MARGINAL VALVE ANATOMY

The anatomy of the valve margins in Herpetocypridinae in general and in *Herpetocypris* in particular bears relics of repeated, probably relatively recent morphological alterations, in this case inward displacement of a selvage. As has been illustrated by several authors, even in the last century (G.W. MÜLLER 1898), Herpetocypridinae have primary and secondary fused zones (Fig. 3E): the pfz (probably the original valve margin) is still recognisable as a marginal zone of non-functional, distally branched, internal structures, which could be called 'false' pore-canals. This zone can be detected with transparent light, but also coincides in some species of *Herpetocypris* with the periferal flattened part of the calcified inner lamella in the LV. Superimposed is the present day functional (secondary) fused zone, in which pore canals bear distal setae; these pore canals are straight along anterior and posterior margins, branched along the ventral margin. This situation is the remnant of a morphological reversal by an inwardly displaced selvage which has later returned to the position of the valve margin; we suggest that the primary fused zone turned atavistic when the selvage superimposed on it.
Also in the LV, the anterior and posterior inner lists are pronounced and ridged. Most likely, these ridges are rem-

nants of pore canals, so that also this inner list is a remnant of a selvage (as is probably often the case in Cyprididae). The present structure is not called a selvage, as no marginal setae occur, one of the best features to distinguish the one structure from the other. The ridges could be a remnant of a tertiary fused zone, although the exact sequence of the different events in which inwardly displacement of selvages has occurred cannot be determined with certainty; names of primary, secondary and tertiary fused zones are therefore tentative.

The RV has a much less developed inner list; the closing mechanism of the valves thus incorporates the valve margin of the RV in-between the valve margin and the pronounced inner list of the LV. The overlap LV over RV is a consequence of this. Some additional sealing is provided by the fact that the inner list of the LV is then effectively positioned in between valve margin and inner list of RV.

CLONAL TAXONOMY: REPRODUCTIVE MODES AND SPECIATION

The four most important contemporary species concepts (Isolation or Biological concept, Phylogenetic concept, Recognition concept and Cohesion concept) rely nearly exclusively on syngamic reproduction. This leaves the taxonomic level of agamically producing entities, mostly clones reproducing by apomictic parthenogenesis (HAVEL & HEBERT 1993), in a nomenclatorial void. There is mounting evidence that ostracod clones (or clusters of closely related clones) can have different and stable morphologies as well as different life histories and a significant number of such clusters of clones in the Cypridoidea (for example in *Heterocypris*, *Herpetocypris*, etc.) were suspected to already have been described as independent species.

The origin of such clones has to be taken into account before deciding about their taxonomic status: such lineages can either remain fully isolated from each other and from possible syngamic populations, or they can occasionally interbreed with syngamic ones. In the first case, these asexual lineages are completely reproductively isolated and could indeed theoretically be considered separate species (ENGHOFF 1976). In the second case, there is no complete reproductive isolation and clones arise either polyphyletically through multiple hybridizations between diploid parent species, or by occasional recurrent interbreeding between sexual and asexual lineages (TURGEON & HEBERT 1995); such lineages should not be considered separate species. The present revision of the genus *Herpetocypris* in Europe aims to contribute to this problem. The discussion will be conducted in full elsewhere, drawing on the data presented in the present paper, but a few general deductions are already formulated here.

The following could be deduced from our database on European *Herpetocypris*: (1) prehensile palps and internal and external anatomy of the hemipenes are identical in all bisexual populations, they thus belong to the same species, *H. brevicaudata*; (2) this species displays a large variability in both valve and non-reproductive soft part anatomy (see below); this variability constitutes a continuous pool, which includes the parthenogenetic populations in the whole of Europe, and no disjunct units can be identified; (3) taxa in which no males have been reported are disjunct units and with limited morphological variability; (4) morphological differences between parthenogenetic species are small, but rather constant.

From the above observations, we conclude that the large and continuous intra-specific variability in the sexual species points towards (occasional) recurrent hybridizations between parthenogenetic females and males, which prevents isolated development of such lineages as morphologically recognisable units. Even if isolated parthenogenetic populations show disjunct morphologies, it follows from investigation of larger numbers of samples that such morphologies fit into a larger and continuous intra-specific variability range. The concept of clonal taxonomy thus appears to be invalid for taxa in which bisexual populations occur. Parthenogenetic lineages with limited variability, on the other hand, can be considered to be separate and disjunct units, even if interspecific differences are small. They constitute morphologically recognisable taxa and can be called species.

ASSESSMENT OF DIAGNOSTIC FEATURES

The taxonomy of the genus *Herpetocypris* has remained confused for a long time, and this for two main reasons: firstly, because the genus has a large morphological uniformity, with few characters showing any difference at all; secondly, because intra-specific variability of characters used was insufficiently known. We will briefly assess the validity of some of the characters used to distinguish species in the past.

Shape and anatomy of valves are often used in ostracods to distinguish species. In *Herpetocypris*, both features are particularly uniform and only small differences in shape and size of the valves occur in the parthenogenetic species, while anatomy of the valve margin is largely identical throughout the genus. Moreover, in *H. brevicaudata*, the only species with syngamic populations, valve shape does vary significantly. This has divided ostracod workers into the two classical camps: lumpers and splitters. Some regarded nearly all species as synonyms of *H. reptans* (GAUTHIER, 1928 a, b), others would consider nearly all populations with slight morphological differences as different species (ROME 1947b, 1954; ANICHINI 1967, 1968a,b). The present revision demonstrates that significant variability must be allowed in taxa with syngamic populations, whereas variability in exclusively parthenogenetic lineages will be much smaller.

Small differences in marginal valve anatomy can occur: the absence of an angle between il and vm in *H. reptans*, the il on the RV closely situated near the valve margin

in *H. mateusorum*, etc. All other species, however, have nearly identical valve anatomies.
Non-reproductive soft part morphology is remarkably uniform. Differences are only found in length of natatory setae (mostly of A2), relative length of Mx2-palp setae and furcal armature.
Length of natatory setae on the A2 has also been used extensively to distinguish species. It is here shown that (1) again larger variability exists in *H. brevicaudata* than in the other species; (2) natatory setae on the A2 should not be considered one character, each seta is a different feature; (3) in some cases the length of one of these setae is species specific (e.g. the 5th seta in *H. reptans*), but in general, and especially in the species with long setae, length of natatory setae can only be used to distinguish species groups.
Length ratios of the apical setae on the Mx2-palp are only useful in the *chevreuxi-helenae-intermedia* group; it is uniform in the other species.
Furcal armature is variable within species, both in size and number of spines per group and number of groups per furcal ramus (Fig. 23). Only *H. chevreuxi* has a special, and probably specific, type of spines (long, straight, blunt) on the furcal ramus. For other species in this genus, this is not a good specific character.

BIOGEOGRAPHY AND EVOLUTION

The extant European *Herpetocypris* species can roughly be divided into 3 groups, based on the length of the natatory setae of the A2: short (mostly not reaching beyond edge of penultimate segment - *H. brevicaudata* and *H. reptans*); intermediate (reaching beyond edge of penultimate segment, but not to tips of claws - *H. mateusorum* and *H. intermedia*) and long (reaching to or beyond tips of endclaws - *H. chevreuxi*, *H. helenae*), although *H. intermedia* resembles the third group in most other aspects of its morphology.
It remains unclear at present if the bisexual species can be regarded as the ancestral root of the genus, from which the other lineages have branched off at different moments in time. This is the most appealing scenario, but there are no facts to support this at present. Although *H. reptans* shares the short natatory setae with *H. brevicaudata*, it differs from it in several other aspects, and a recent origin of *H. reptans* from the *H. brevicaudata* root seems unlikely. There is a second argument to consider *H. reptans* a relatively old species. MARTENS (in press) suggested that the genus *Humphcypris*, also belonging in the Herpetocypridinae, with c 15 species in Africa, Asia and the Levant, originated in the eastern basin of the Mediterranean from a *Herpetocypris*-like ancestor with short natatory setae on the A2. Interestingly, in most species of *Humphcypris,* the first natatory seta is the longest. This is as in *H. reptans*, not as in *H. brevicaudata.* If *H. reptans* and *Humphcypris* share the same ancestor, then *H. reptans* must be one of the older species in the genus.
Herpetocypris mateusorum is a special case, with valve shape rather similar to *H. brevicaudata* and with special anatomy of the valve margin. Moreover, this species appears to be endemic to the western part of the Iberian peninsula. It could be a recent spin-off from the *H. brevicaudata* lineage.
Origin and age of the *chevreuxi-helenae-intermedia* lineage, finally, is unclear. The three species are closely related and one could even argue that they should be considered as subspecies of one species. However, this would needlessly complicate matters and as they are not geographically segregated, we here keep them at specific level. As far as can be judged to date, *H. helenae* seems to have the widest distribution.

Conclusion

Considering the possible effect of reproductive mode on morphological variability has facilitated the revision of one of the most difficult genera in European non-marine Ostracoda. Six extant species are retained, one Pleistocene species must be considered extinct. In order to reach an understanding of the general evolutionary patterns within this genus, the same concept should be applied to *Herpetocypris* from other parts of the world (North America, Asia).

Acknowledgements

We thank J. CILLIS and C. BEHEN (Brussels) for technical assistance with the SEM and the line drawings, respectively. For assistance with the 1996 sampling trip to Portugal, the senior author thanks J. IZQUIERDO, I. PRIETO and P. ALCORLO (Madrid). Other new material and museum collections were obtained with the help of K. WOUTERS and B. GODDEERIS (Brussels), E. PIETRZENIUK (Berlin), M. CHRISTIANSEN (Oslo), B. HAUSER (Genève), A. MORGAN (London), R. VONK (Amsterdam), H.J. DUMONT (Ghent), M. MARTINO (Porto) and D.J. HORNE (Chatham). Translation of texts were provided by I. SCHÖN (Leeds), T. VANDEKERCKHOVE and A. VAN DE WEGHE (Ghent) and V. ARKOSI (Brussels). Dr K. WOUTERS is especially acknowledged for editorial assistance. Un agradecimiento especial a mi madre (M.G). This work has been supported by the E.U. Human Capital and Mobility Program (contract ERBCHRXCT/93/0253).

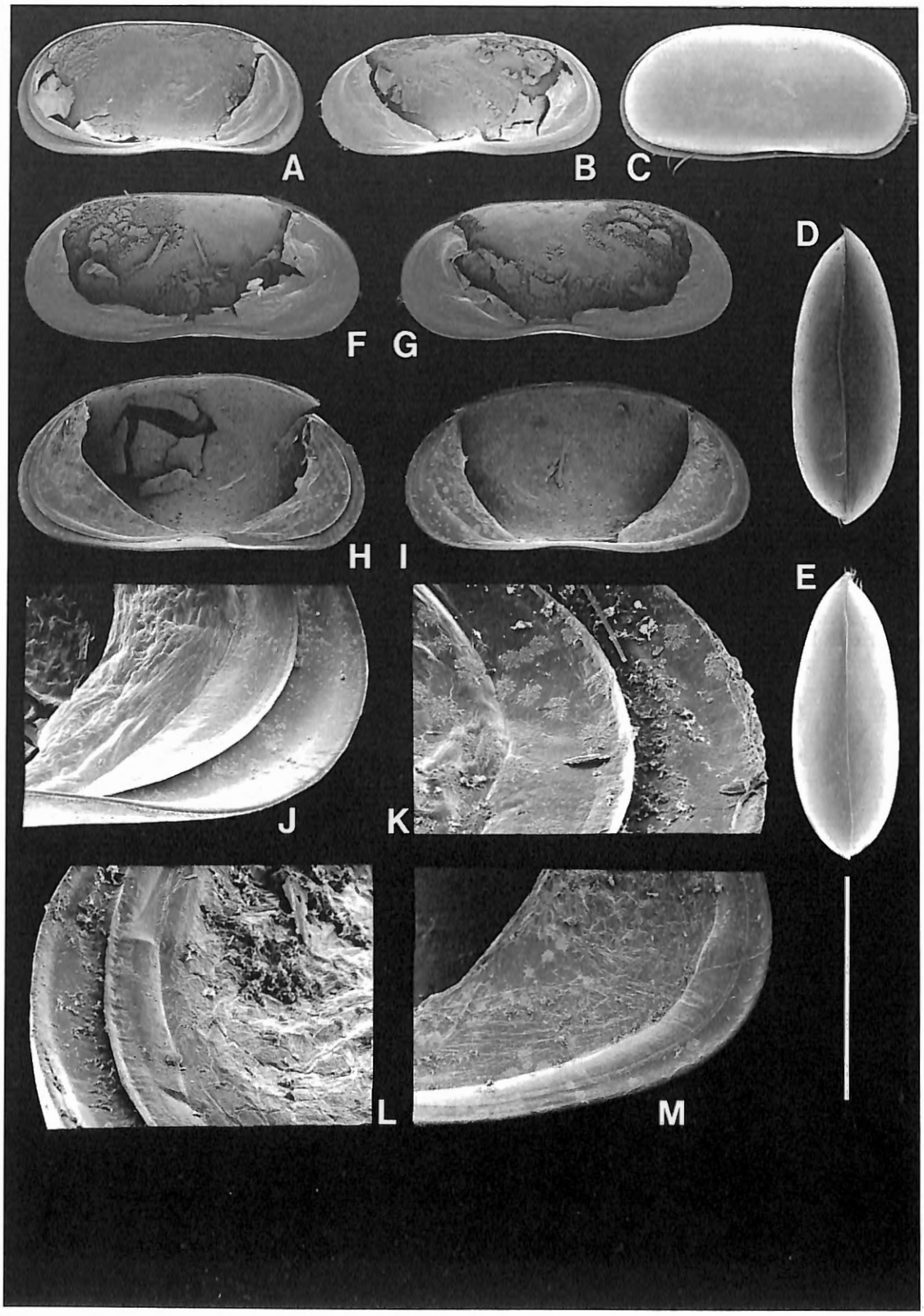

Fig. 18. – *Herpetocypris reptans* (A-E, adult; F-G, (A-1) juvenile; J, adult; female, Belgium), *Herpetocypris reptans curvata* (H-I, K-N, type, female, Swizerland).
A. *LV, internal view (OC.1894).* B. *RV, internal view (OC.1894).* C. *Cp, right lateral view (OC.1893).* D. *Cp, ventral view (OC. 1893).* E. *Cp, dorsal view (OC. 1893).* F. *LV, internal view (OC.1898).*G. *RV, internal view (OC.1898).* H. *LV, internal view (MG145).* I. *RV, internal view (MG145).* J. *LV, detail anterior margin (OC.1894).* K. *LV, detail anterior margin (MG145).* L. *RV, detail anterior margin (MG145).* M. *RV, detail posterior margin (MG145).*
Scale: 100 µm for L; *200 µm for* K; *500 µm for* J, M; *1220 µm for* F-G; *1410 µm for* H-I; *1790 µm for* A-E.

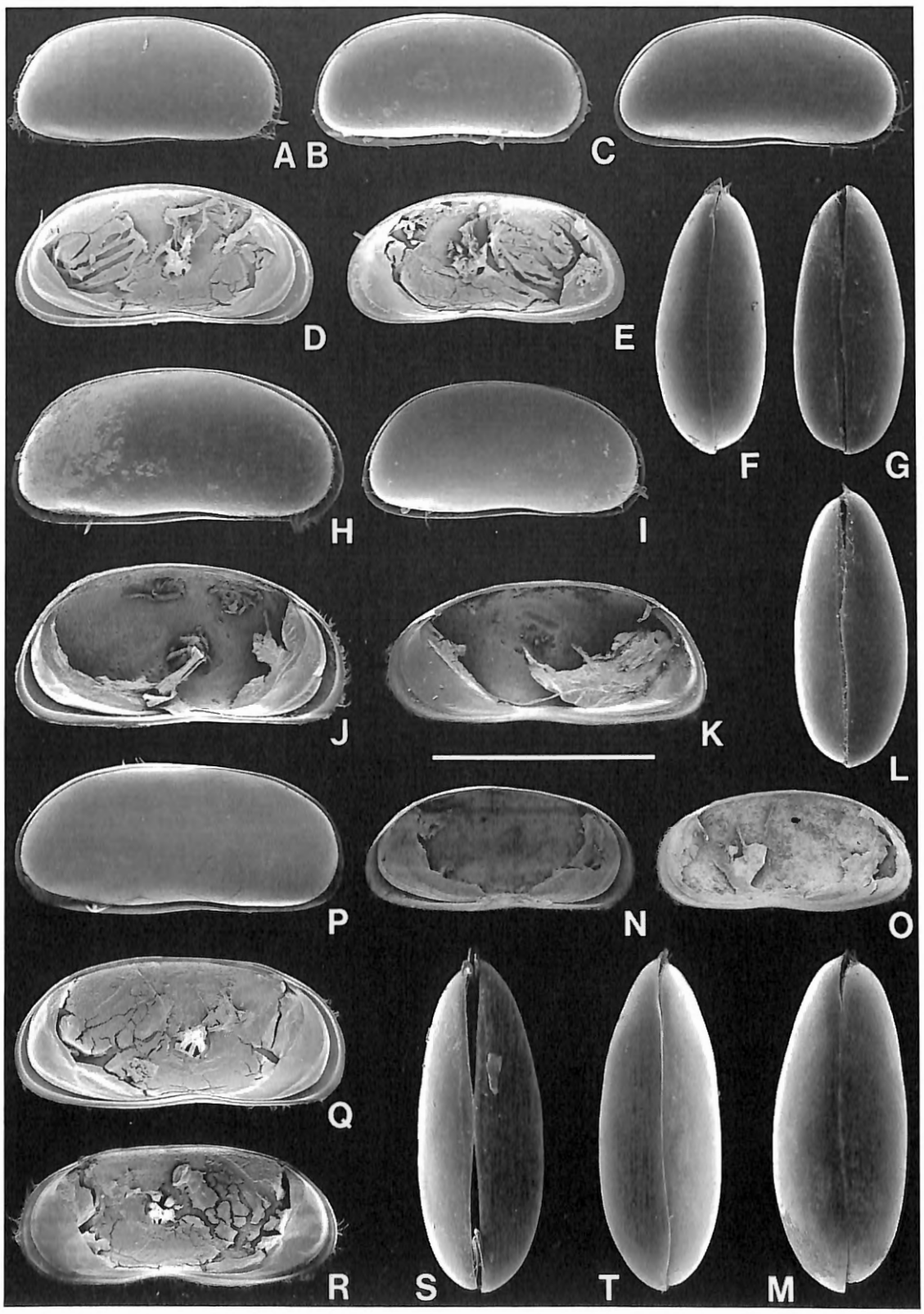

Fig. 19. – *Herpetocypris brevicaudata* (males and females).(D-T: Belgium, A-M: Algeria). *Herpetocypris ghigii* (N-O, type, female, Morocco).
A. *Cp, right lateral view (OC.1992).* B. *Cp, right lateral view (OC.1982).* C. *Cp, right lateral view (OC.1958).* D. *LV, internal view (OC. 1983).* E. *RV, internal view (OC. 1983).* F. *Cp, dorsal view (OC.1992).*G. *Cp, ventral view (OC.1992).* H. *Cp, right lateral view (OC.1958).* I. *Cp, right lateral view (OC.1981).* J. *LV, internal view (OC.1963).* K. *RV, internal view (OC. 1963).* L. *Cp, ventral view (OC.1958).* M. *Cp, ventral view (OC.1958).* N. *LV, internal view (KM1388).* O. *RV, internal view (KM1388).* P. *Cp, right lateral view (OC.1952).* Q. *LV, internal view (OC. 1950).* R. *RV, internal view (OC. 1950).* S. *Cp, ventral view (OC.1956).*T. *Cp, dorsal view (OC.1952).*
Scale: 1090 µm for A-E; *1160 µm for* F-M; *1250 µm for* P-T; *1520 µm for* N-O.

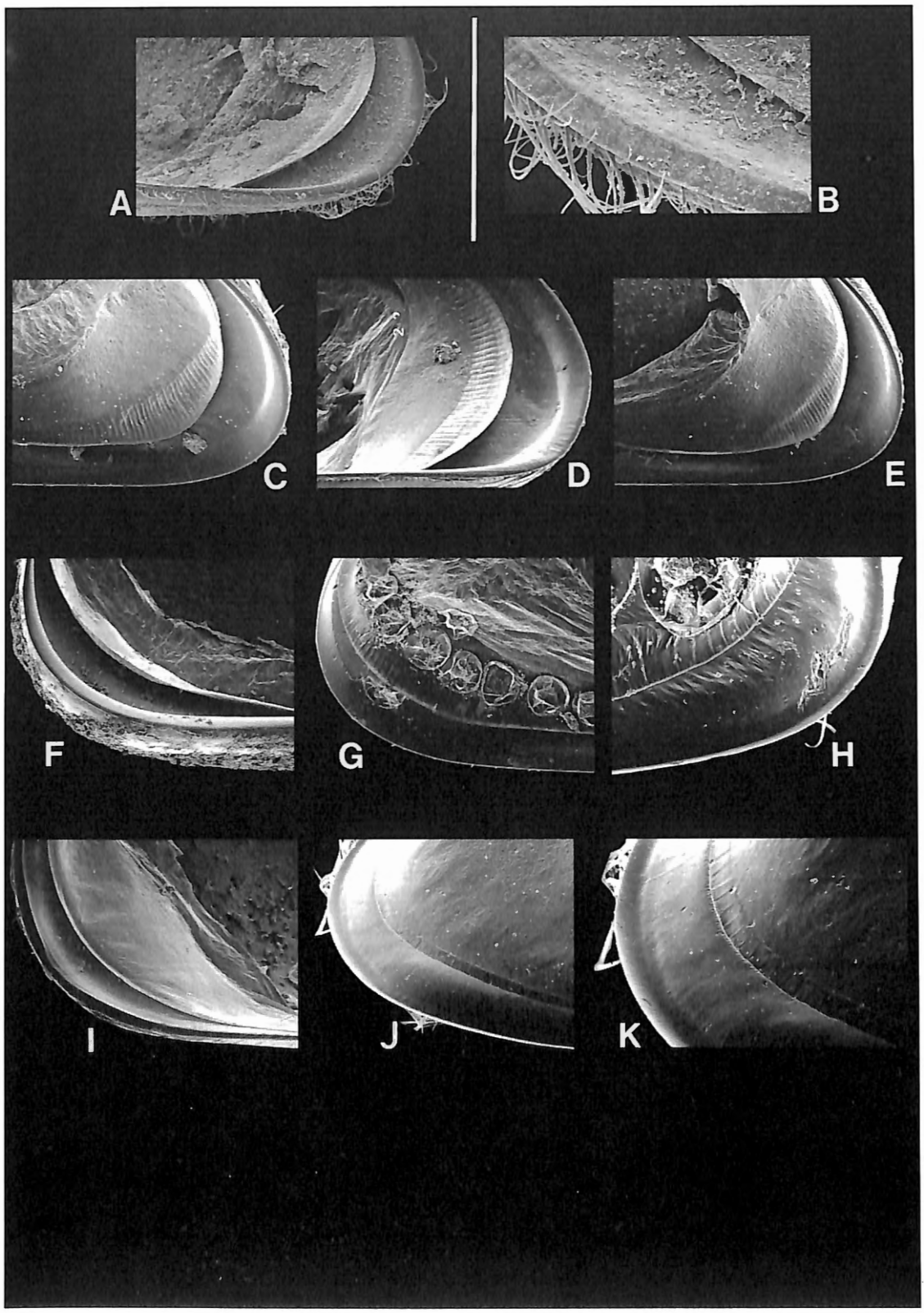

Fig. 20. – *Herpetocypris brevicaudata* (males and females).(Algeria).
A. *LV, detail anterior margin (KM1388).* B. *RV, detail anterior margin (KM1388).* C. *LV, detail anterior margin (OC.1994).* D. *LV, detail anterior margin (OC.1986).* E. *LV, detail anterior margin (OC.1995).* F. *LV, detail posterior margin (OC.1963).* G. *LV, detail posterior margin (OC.1995).* H. *RV, detail posterior margin (OC.1995).* I. *RV, detail anterior margin (OC.1986).* J. *RV, detail anterior margin (OC.1994).* K. *RV, detail anterior margin (OC.1994).*
Scale: 91 µm for B; *114 µm for* H; *227 µm for* J; *228 µm for* I; *312 µm for* C, E; *347 µm for* D; *410 µm for* A.

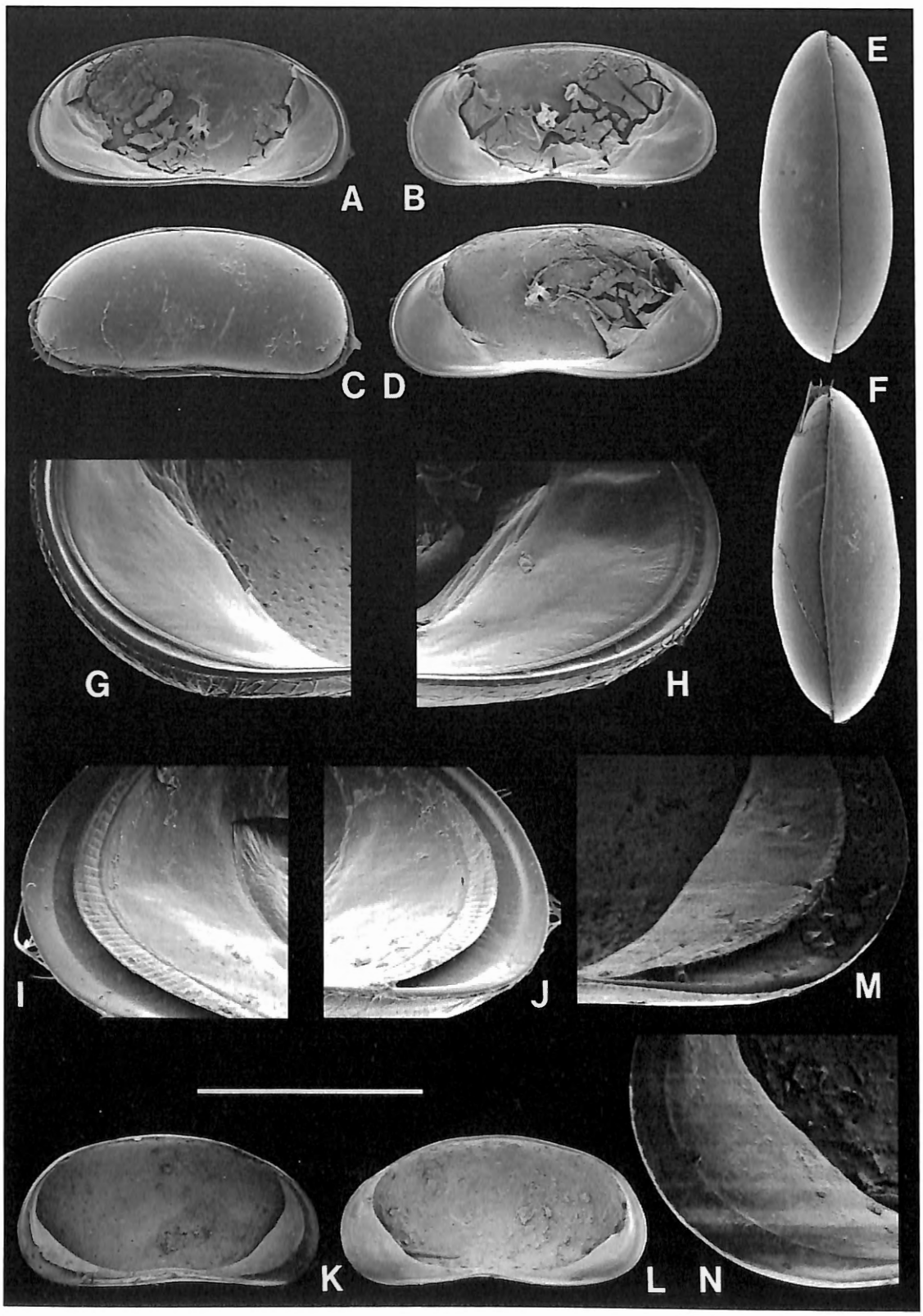

Fig. 21. – *Herpetocypris mateusorum* (A-J, Portugal), *Herpetocypris ehringdorfensis* (K-N, Pleistocene, Germany).
A. *LV, internal view (OC.1941).* B. *RV, internal view (OC.1941).* C. *Cp, right lateral view (OC.1944).* D. *RV, internal view (OC. 1943).* E. *Cp, dorsal view (OC. 1944).* F. *Cp, ventral view (OC.1944).*G. *RV, detail anterior margin (OC.1943).* H. *RV, detail posterior margin (OC.1943).* I. *LV, detail posterior margin (OC.1945).* J. *LV, detail anterior margin (OC.1945).* K. *LV, internal view (665/54).* L. *RV internal view (665/54).* M. *LV, detail anterior margin (665/54).* N. *LV, detail anterior margin (665/54).*
Scale: 320 μm for G, I, J, M, N; *338 μm for* H; *1250 μm for* A-F, K, L.

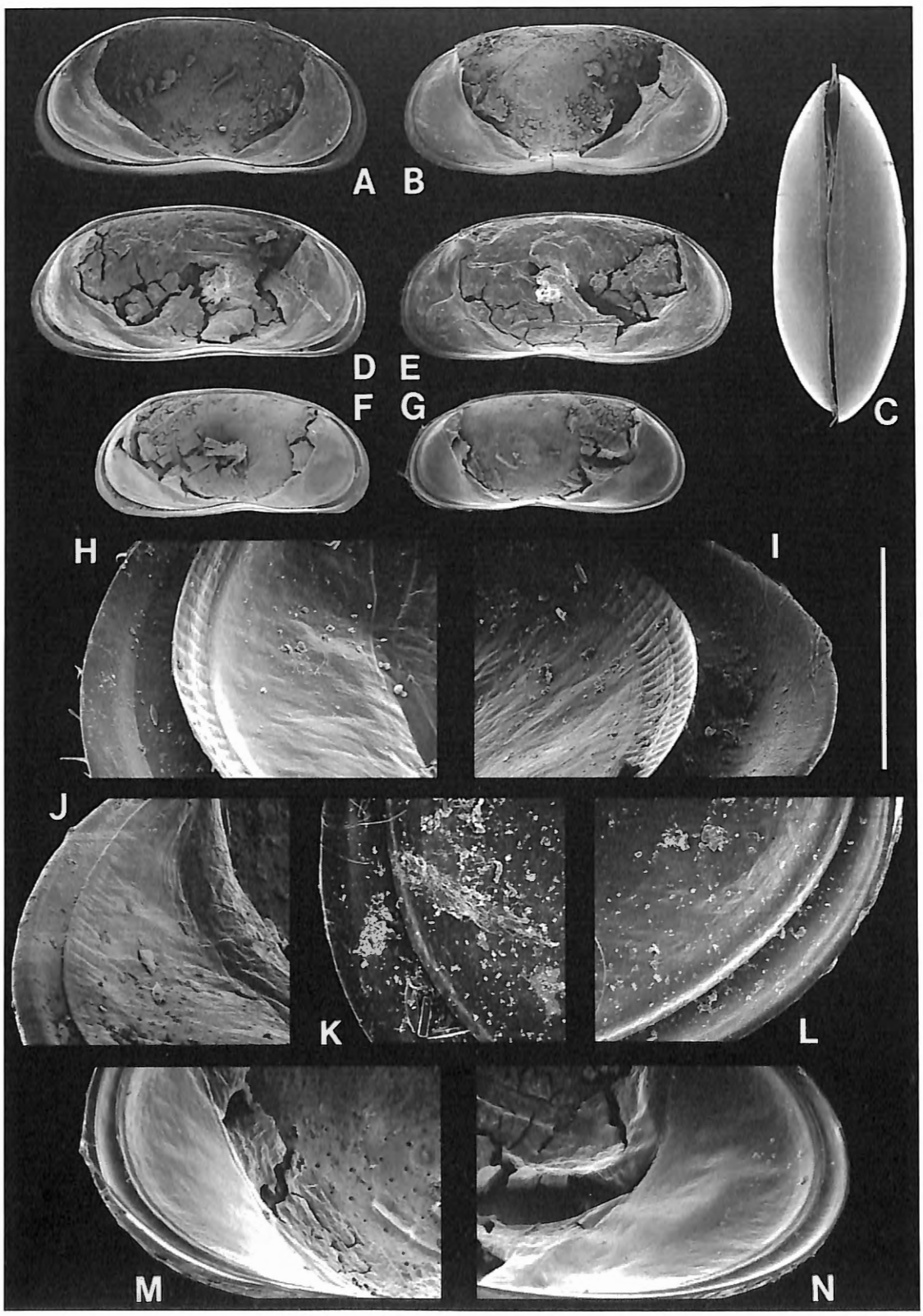

Fig. 22. – *Herpetocypris intermedia* (A-C, M-L, type, Switzerland); D,E, Spain; F, G, M, N, Algeria).
A. *LV, internal view (MG140).* B. *RV, internal view (MG140).* C. *Cp, ventral view (MG144).* D. *LV, internal view (OC.1946).* E. *RV, internal view (OC.1946).* F. *LV, internal view (OC.1988).* G. *RV, internal view (OC.1988).* H. *LV, detail posterior margin (MG140).* I. *LV, detail anterior margin (MG140).* J. *RV, detail anterior margin (MG140).* K. *RV, detail anterior margin (MG140)* L. *RV, detail posterior margin (MG140).* M. *RV, detail anterior margin (OC.1988).* N. *RV, detail posterior margin (1988).*
Scale: 175 µm for H, I, J, K, L; *320 µm for* M, N; *1219 µm for* A-G.

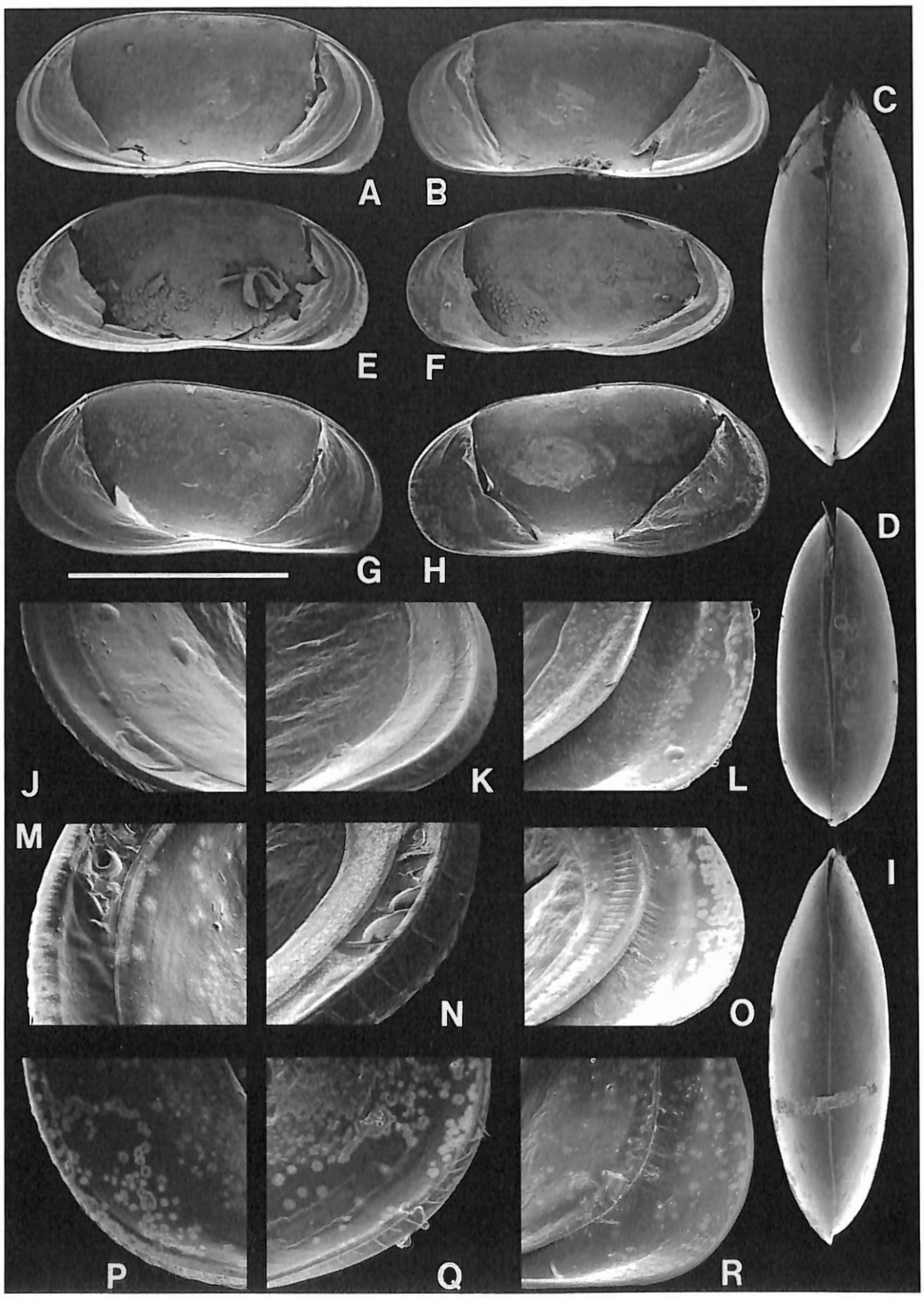

Fig. 23. – *Herpetocypris chevreuxi* (female, A-D, G-L, P-R, Belgium; E, F, M-O, type, Algeria).
A. *LV, internal view (OC.1925).* B. *RV, internal view (OC.1925).* C. *Cp, dorsal view (OC.1924).* D. *Cp, ventral view (OC.1924).* E. *LV, internal view (MG128).* F. *RV, internal view (MG128).* G. *LV, internal view (OC.1935).* H. *RV, internal view (OC.1935).* I. *Cp, dorsal view (OC.1940).* J. *RV, detail anterior margin (OC.1925).* K. *RV, detail posterior margin (OC.1925).* L. *LV, detail anterior margin (OC.1925).* M. *RV, detail anterior margin (MG128)* N. *RV, detail posterior margin (MG128).* O. *LV, detail anterior margin (MG128).* P. *RV, detail anterior margin (OC.1935).* Q. *RV, detail posterior margin (OC.1935).* R. *LV, detail anterior margin (OC.1935).*
Scale: 175 µm for M, N; *320 µm for* J-L, O-R; *1299 µm for* A-I.

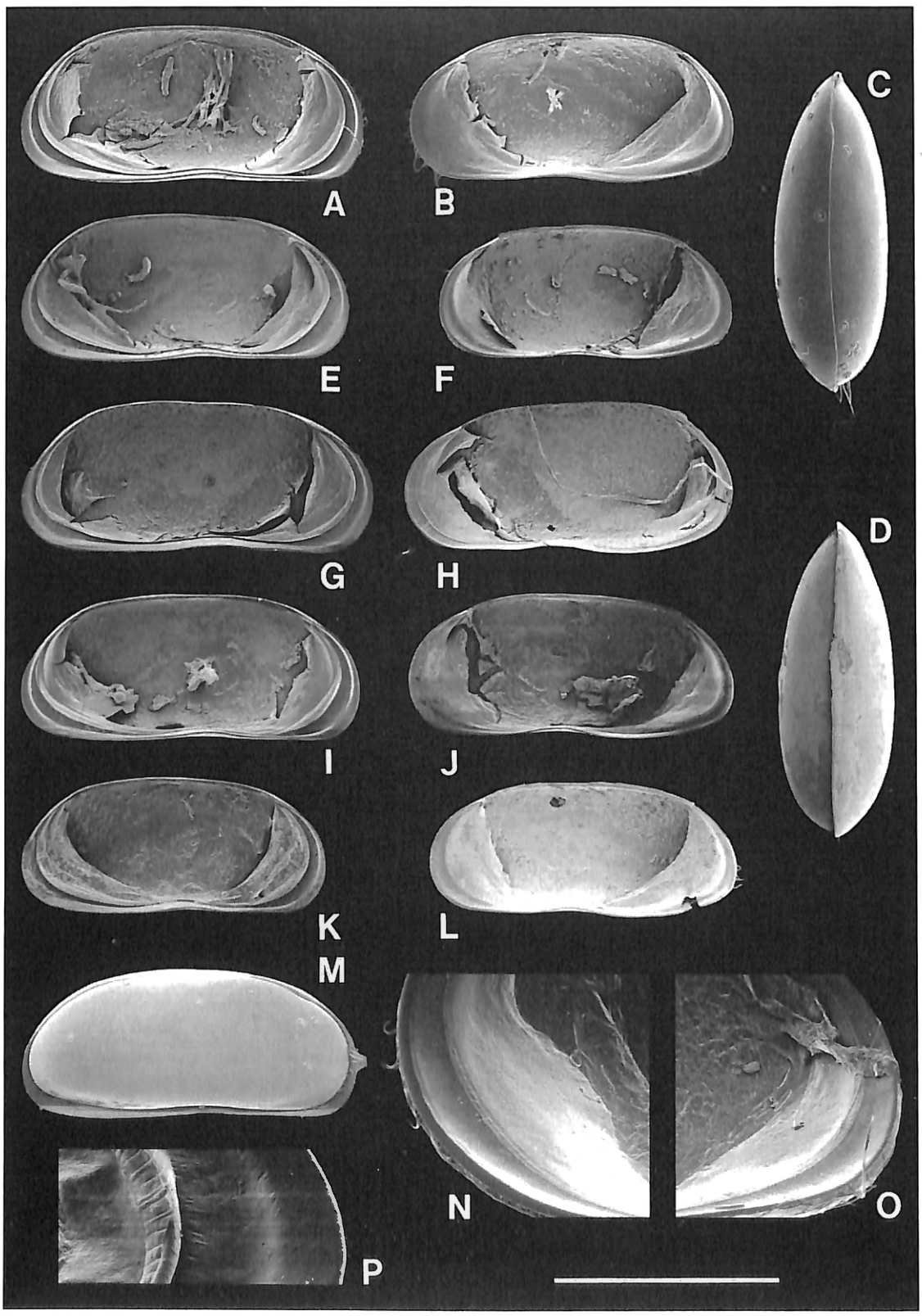

Fig. 24. – *Herpetocypris helenae* (female; A-D, M-O, South Africa; I, F, Israel). *Herpetocypris caerulea* (female type; G, H, P, Belgium). *Herpetocypris palpiger* (female type; I, J, Belgium). *Herpetocypris intermedia latialis* (female type; K, L, Italy). A. *LV, internal view (OC.1910)*. B. *RV, internal view (OC.1910)*. C. *Cp, dorsal view (OC.1911)*. D. *Cp, ventral view (OC.1912)*. E. *LV, internal view (OC.1918)*. F. *RV, internal view (OC.1918)*. G. *LV, internal view (MG131)*. H. *RV, internal view (MG131)*. I. *LV, internal view (MG130)*. J. *RV, internal view (MG130)*. K. *LV, internal view (MG129)*. L. *RV, internal view (MG129)*. M. *Cp, right lateral view (OC.1913)*. N. *RV, detail anterior margin (OC.1904)*. O. *RV, detail posterior margin (OC.1904)*. P. *LV, detail anterior margin (MG131)*.
Scale: 175 µm for P; *320 µm for* N-O; *1315 µm for* M; *1410 µm for* A-L.

References

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APPENDIX: material used for the present revision

Herpetocypris reptans
Herpetocypris reptans reptans

- KBIN-OC.: Harchies (Belgium) 50°32'N 3°51'E. Coll.: G. MARLIER, 1-09-1977.(Dissected specimen: W1043). (IG.25544). (D135)
- KBIN-OC.: Prinsenpark Retie (Belgium) 51°16'N 5°05'E. Coll.: K. WOUTERS, 26-12-1976. (Dissected specimen: W1004). (IG.25300). (D44).
- KBIN-OC.: Heverlee (Belgium) 50°52'N 4°42'E. Coll.: GERARD, 27-10-1986. (Dissected specimen: W1683). (IG.26985).
- KBIN-OC.: Mirwart (Belgium) 50°03'N 5°16'E. Coll.: D. PIERRE, 1970. (Dissected specimens: IG.24443, IG.24326).
- KBIN-OC.: Rouge Cloître, near Brussels (Belgium) 50°50'N 4°21'E. Coll.: R.M. ROME, 28-05-1941. (Dissected specimen: IG.13125).
- KBIN-OC.: Woumen 'De Blankaart' (Belgium) 51°00'N 2°52'E. Coll.: B.G. GODDEERIS, 3-07-1977. (Dissected specimen: W1028). (IG.25756). (D82).
- KBIN-OC. 1893-1897: De Pinte (Belgium) 50°59'N 3°39'E. Coll.: D. ROELS, 1986. (Dissected specimens and valves: MG053-056, MG089-091, KM1358).
- KBIN-OC. 1898: Lake Donk (Belgium) 50°57'N 5°08'E. Coll.: K. MARTENS, 28-03-84. (Dissected specimen: KM899). (D16-1).

Herpetocypris reptans curvata

- MHNG: Mendriso (Switzerland) 45°53N 8°59'E. Coll.: KAUFMANN. (Dissected specimen: MG139).

Herpetocypris brevicaudata

- KBIN-OC. 1947-1952: Vlierzele (Belgium) 50°56'N 3°54'E. Coll.: K. MARTENS, 15-09-1988. (Dissected specimens and valves: MG017-021, MG037-039).
- KBIN-OC.: Spy-Mornimont (Belgium) 50°29'N 4°43'E. Coll. 9-06-1950. (Dissected specimen: W1629). (IG.17098).
- KBIN-OC. 1953-1957: Andenne (Belgium) 50°29'N 5°06'E. Coll.: K. MARTENS, 19-11-1983. (Dissected specimens: KM895, KM896, MG066, MG078-081, MG120-121, W1506. (IG.26718). (D704).
- KBIN-OC. 1958-1960, 1963: Oued Dfali (Algeria) 34°51'N 1°22'W. Coll.: GAGNEUR, 8-11-86. (Dissected specimens: KM1346, MG028-033). (IG.27699).
- KBIN-OC. 1961: Oued Dfali (Algeria) 34°51'N 1°22'W. Coll.: GAGNEUR, 13-05-87. (Dissected specimen MG063). (IG.27699).
- KBIN-OC. 1962: Oued Dfali (Algeria) 34°51'N 1°22'W. Coll.: GAGNEUR, 29-01-87. (Dissected specimen: MG088). (IG.27699).
- KBIN-OC. 1964: Oued Bel Abbes (Imama) (Algeria) 34°52'N 1°21'W, Coll.: GAGNEUR, 29-01-87. (Dissected specimens and valves: MG060). (IG.27699).
- KBIN-OC. 1965: (males present), waterhole Ghar Boumaza (Algeria) 34°41'N 1°18'W, Coll.: GAGNEUR, 05-05-88. (Dissected specimens MG092-093). (IG.27699).
- KBIN-OC. 1967: Oued Rediou, Honaïne (Algeria), Coll.: GAGNEUR, 24-4-87. (Dissected specimen MG062). (IG.27699).
- KBIN-OC. 1968: Oued Saf-Saf (Algeria) 34°51'N 1°15'W, Coll.: GAGNEUR, 26-09-86. (Dissected specimen: MG027). (IG.27699).
- KBIN-OC. 1969: Oued Saf-Saf (Algeria) 34°51'N 1°15'W, Coll.: GAGNEUR, 13-05-87. (Dissected specimen: MG035). (IG.27699).
- KBIN-OC. 1970: Oued Saf-Saf (Algeria) 34°51'N 1°15'W, Coll.: GAGNEUR, 9-11-86. (Dissected specimen:MG061). (IG.27699).
- KBIN-OC. 1971-1973: Oued Sebdou 34°37'N 1°21'W (Algeria). Coll.: GAGNEUR, 22-07-1983, sample T3-SI-1. (Dissected specimens: KM900-902).
- KBIN-OC. 1974: Oued Sebdou 34°37'N 1°21'W, Algeria. Coll.: GAGNEUR, 1983, (Dissected specimen: MG065).
- KBIN-OC. 1975: Source de la Tafna (Algeria) 34°42'N 1°18'W, Coll.: GAGNEUR, 13-6-1989. (Dissected specimen: KM1516). (IG.27699).
- KBIN-OC. 1976-1987: Aïn El Haman St. 6-7, (Algeria) 36°34'N 4°2'E. Coll.: H. DUMONT, 18-01-1988. (Dissected specimens and valves: KM383-387, MG044-049, MG075-077, MG082-086).
- KBIN-OC. 1989: Mts. Tassili N'Ajjer (Algeria). Coll.: BOUVET, 16-10-1981, St.10. (Dissected specimen: KM381).
- KBIN-OC. 1990-1991: (males present). W. Tlemcem, Aïn Badelos, (Algeria), 34°41'N 2°42'W. Coll.: Amsterdam expedition, 16-04-1983. Sample 83-20. (Dissected specimens: KM187-188).
- KBIN-OC. 1992-1995: (males present), W. Saïda, (Algeria) 34°54'N 0°13'W. Coll.: Amsterdam expedition, 27-04-1983. Sample 83-71. (Dissected specimens and valves: MG067-074).
- KBIN-OC. 1996: W. Saïda, Ben-Ikhou 32°36'N 0°51'W (Algeria). Coll.: Amsterdam expedition, 2-05-1983. Sample 83-97 (Dissected specimen: MG109).
- KBIN-OC. 1997: W. Tlemcen, Ochba (Algeria) 34°54'N 1°15'W. Coll.: Amsterdam expedition, 17-04-1983. Sample 83-28. (Dissected specimen: MG110).
- KBIN-OC. 2000-2001: stream near (4Km) Ledesma (Spain) 41°05'N 6°00'W. Coll.: M.G. GONZALEZ-MOZO & P. ALCORLO, 18-04-1996. (Dissected specimens: MG146-147). (MP-59).
- AMST. EXPED.: W. Tlemcen, valley of Oued Chouly (Algeria) 34°45N 1°12'W. Coll.: Amsterdam expedition, 14-04-1983. Sample 83-4. (Valves MG034, MG087).
- AMST. EXPED.: W. Tlemcen, Tafna (Algeria) 34°41N 1°18'W. Coll.: Amsterdam expedition, 20-04-1983. Sample 83-43. (Dissected specimens: MG101-102).
- AMST. EXPED.: W. Saïda (Algeria) 34°48'N 0°6'E. Coll.: Amsterdam expedition, 28-04-1983. Sample 83-78. (Dissected specimen: MG103).
- AMST. EXPED.: W. Saïda (Algeria) 34°48'N 0°11'E. Coll.:Amsterdam expedition, 28-04-1983. Sample 83-76. (Dissected specimen: MG111).
- AMST. EXPED.: (males present). W.Tlemcem, Aïn Badelos, (Algeria),34°41'N 2°42'W. Coll.: Amsterdam expedition, 16-04-1983. Sample 83-20. (Dissected specimen: MG106).
- AMST. EXPED.: W. Tlemcen, Ghazaouet 35°6'N 1°45'W (Algeria). Coll.: Amsterdam expedition, 18-04-1983. Sample 83-35. (Dissected specimen: MG107).
- AMST. EXPED.: W. Tlemcen, S of Bouda (Algeria) 34°34'N 2°43'W. Coll.: Amsterdam expedition, 16-04-1983. Sample 83-17b. (Dissected specimen: MG108).
- AMST. EXPED.: W. Tlemcen, Ochba (Algeria) 34°54'N 1°15'W. Coll.: Amsterdam expedition, 17-04-1983. Sample 83-28. (Dissected specimens: MG112-113).
- AMST. EXPED.: (males present), W. Tlemcen, Aim Essouk (Algeria) 34°49'N 1°6'W. Coll.: Amsterdam expedition, 16-04-1983. Sample 83- 23. (Dissected specimens: MG116-117).

-AMST. EXPED.: (males present), W. Tlemcen, Tafsout 35°12'N 1°39'W. Coll.: Amsterdam expedition, 15-04-1983. Sample 83-16. (Dissected specimens: MG114-115). - BALTANAS collection: (males present), source in Pilar del Mono, Durcal 37°00'N 3°34'W (Granada, Spain). Coll.: J. TEMPLADO & D. MORENO, 17-10-1989. (FCu-494).
- BALTANAS collection: stream around the center of the Caserio de San Bernardino (Cadiz, Spain) 36°32'N 6°18'W. Coll.: A. BALTANAS, 7-04-86. (Dissected specimen: Ref.29).
- BALTANAS collection: pond in Costurera (Badajoz, Spain) 38°53'N 6°58'W. Coll.: FERNANDEZ-LOPEZ, 4-01-86. (Dissected specimens: Ref. 37, Ref.38).
- BALTANAS collection: spring in Pirineos (Spain). Coll.: J.R. ROCA. (Dissected specimen: Ref. 159).
- BALTANAS collection:Ança (Coimbra, Portugal) 40°12'N 8°25'W. Coll.: A. BALTANAS, 14-12-1986. (Dissected specimen: Ref. 104).
- BALTANAS collection: 'gravera' of the Ebro River in Flix (Tarragona, Spain) 41°07'N 1°15'E. Coll.: A. BALTANAS, 28-03-1990. (Dissected specimen: Ref. 259).
- BALTANAS collection 88CO20PI8, Canada. Coll.: R.M. FORESTER. (Dissected specimens: MG059, MG100).
- BALTANAS collection: Magre River in Valencia St. MR7 (Hortones de Arriba).(Spain) 39°29'N 0°24'W. Coll.: MEZQUITA, 3-4-June 1995. (Dissected specimens and valves: MG040-43, MG057).

Herpetocypris chevreuxi

- KBIN-OC.: De Westhoek, De Panne (Belgium) 51°06'N 2°35'E. Coll.: TAVERNIER, 23-08-1980. (Dissected specimens: W1128-1193). (IG.26061).
- KBIN-OC.: De Panne (Belgium) 51°06'N 2°35'E. Coll.: R.P. ROME, 22-09-1902. (IG9302)
- KBIN-OC.: Houtsaegersduinen, De Panne (Belgium) 51°06'N 2°35'E. Coll.: GODDEERIS, 22-09-1978.(Dissected specimen: W1041). (IG.25758).
- KBIN-OC.: Woumen, Blankaart (Belgium) 51°00'N 2°52'E. Coll.: K. WOUTERS, 4-04-1981. (Dissected specimen: W1321). (IG.26212). (D328).
- KBIN-OC. 1923-1925: waterspaarbekken in Woumen, Blankaart (Belgium) 51°00'N 2°52'E. Coll.: B. GODDEERIS, 20-11-1995 (Dissected specimens and valves: MG122, MG124-127).
- KBIN-OC. 1926: Horto das Virtudes (Porto, Portugal) 41°09'N 8°37'W. Coll.: L. PAULO. (Dissected specimens: MG133).
- KBIN-OC. 1927: Navalmoral (Caceres, Spain) 40°27'N 4°45'W. Coll.: A. BALTANAS, 1992. (Dissected specimen: GR003).
- KBIN-OC. 1928: Hoboken Polder (Belgium) 51°11N 4°21'E. Coll.: K. MARTENS, 16-8-1980. (Dissected specimens: KM897).
- KBIN-OC. 1929: En Tamar OST1554 (Israel) 30°75'N 35°21'E. Coll.: R. ORTAL, 16-12-1980. (Dissected specimen: KM733).
- KBIN-OC. 1930: Oasis Cufra. Coll.: LEONARD, 5-1-1965. (Dissected specimens: KM898).
- KBIN-OC. 1931: Mts. Tassili N'Ajjer (Algeria). Coll.: BOUVET, 15-10-1981, St.9. (Dissected specimens: KM378).
- KBIN-OC. 1934: Lake Hula (Israel) 33°07N 35°38'E. Coll.: 12-03-1990 (Dissected specimen: KM1340).
- KBIN-OC. 1935-1940: De Panne (Belgium). Coll.: TAVERNIER, 23-08-80. (Dissected specimens and valves: MG022-026, MG123).
- BALTANAS collection: pond in Bohonoal de Ibor (Caceres, Spain) 39°47'N 5°28'W. Coll.: A. BALTANAS, 15-03-1986 (Dissected specimen: Ref. 14). - BALTANAS collection: pond in the road Plasencia to Navalmoral, Finca Castillo, Caceres (Spain) 39°29'N 6°23'W. Coll.: A. BALTANAS, 26-04-1986. (Dissected specimen: Ref. 87).
- BALTANAS collection: pond in the road Caceres to Merida (Spain) 38°55'N 6°20'W. coll: A. BALTANAS, 27-04-1986. (Dissected specimens: Ref. 70, Ref. 78).
- BALTANAS collection: Quintanar de la Serena (Badajoz, Spain) 38°53'N 6°58'W. Coll.: FERNANDEZ-LOPEZ, 24-05-1986 (Dissected specimens: Ref. 60-62).
- BALTANAS collection: Quintanar de la Serena (Badajoz, Spain) 38°53'N 6°58'W. Coll.: FERNANDEZ-LOPEZ, 16-03-1986 (Dissected specimen: Ref. 81).
- BALTANAS collection: pond in Robledillo de la Vera (Spain). Coll.: A. BALTANAS, 25-05-1986. (Dissected specimen: Ref. 86).
- BALTANAS collection: pond in an olive plantation in the road of Torrejon el Rubio to Caceres (Spain) 39°46'N 6°01'W. Coll.: FERNANDEZ-LOPEZ, 27-04-1986 (Dissected specimens: Ref. 20-21).
- BALTANAS collection: pond in Torrejon el Rubio (Caceres, Spain) 39°46'N 6°01'W. Coll.: FERNANDEZ-LOPEZ, 05-04-1986 (Dissected specimen: Ref. 91).
- NORMAN collection: type material 'swamp in Bon Kamera, (Kharezas)' in Bona (Algeria). Coll.: M.E. CHEVREUX, 6/8-07-1895 (Dissected specimen: MG128).
- ZMO.F22578. Algier (Algeria) 36°50'N 3°00Ë. Coll.: SARS, 1898. (Dissected specimen: MG148).

Herpetocypris intermedia

- KBIN-OC. 1945: rice field in Coimbra (Portugal) 40°12'N 8°25'W. Coll.: A. BALTANAS, 26-06-1988 (Dissected specimen: GR008).
- KBIN-OC. 1946: Sangrera River, San Bartolomé de las Abiertas 39°50'N 4°44'W, (Toledo, Spain). Coll.: A. BALTANAS. (Dissected specimen: GR006).
- KBIN-OC. 1988: Mts. Tassili N'Ajjer (Algeria). Coll.: BOUVET, 15-10-1981, St.9. (Dissected specimen: KM377).
- BALTANAS collection: rice field in Coimbra (Portugal) 40°12'N 8°25'W. Coll.: A. BALTANAS, 26-06-1988 (Dissected specimen: Ref. 266).
- MHNG: Mendriso (Switzerland) 45°53'N 8°59'E. Coll.: KAUFMANN. (Dissected specimen: MG140).

Herpetocypris mateusorum

- KBIN-OC. 1941-1944: spring in Fornos do Algodres 40°38'N 7°32'W (Portugal). Coll.: M.G. GONZALEZ-MOZO & P. ALCORLO, 14-04-1996 (Dissected specimens: MG135-137, valves: MG141-143). (MP-39).
- BALTANAS collection: pond in Puerto de Conejeros (Badajoz, Spain) 38°53'N 6°58'W. Coll.: FERNANDEZ-LOPEZ, 4-11-1985 (Dissected specimens: Ref. 17, 22, 25).

Herpetocypris agilis (= Herpetocypris chevreuxi)

- KBIN-OC.: type material: Egenhoven (Leuven), 50°53N 4°42'E. (Belgium). Coll.: D.R. ROME, 02-1947.

Herpetocypris caerulea (= Herpetocypris helenae)

- KBIN-OC.: type and paratype material: pond in the Botanical Garden of Leuven (Belgium) 50°53N 4°42'E. Coll.: ROME, 6-10-1945 (Dissected specimens: W1129, MG131). (IG19548).

Herpetocypris intermedia var *latialis (= Herpetocypris helenae)*

- NORMAN collection Lean n° CR96/12T: co-type material Rome (Italy) 41°53'N 12°30'E. Coll.: MASI. (Dissected specimen: MG129).

Herpetocypris palpiger (= Herpetocypris helenae)

- NORMAN collection Lean n° CR96/12T co-type material: Corsham (England) 51°26'N 2°11'W. Coll.: A.Q. LOWNDES, 1931 (Dissected specimens: MG130, MG132).

Herpetocypris helenae

- KBIN-OC. 1899-1916: Macasse (South Africa) 34°05'N 18°51'E. Coll. K. MARTENS, 5-02-1989. (Dissected specimens: MG001-007, MG012-013, MG015-016, MG050-052, MG119, KM1352-1354).
- KBIN-OC. 1917,1919: Sa'Ad 31°28'N 34°32'E (10 Km S of Jerusalem, Judean mountains) (Israel) St. 2,12. Coll.: DECU, 17-05-1990 (Dissected specimens: MG094, MG096). (Det. as *Herpetocypris chevreuxi*).
- KBIN-OC. 1918: En Bikkora (Jerusalem, Israel) 31°47'N 35°13'E. Coll.: DECU, 24-05-1990. St. 6. (Dissected specimen: MG095). (Det. as *Herpetocypris chevreuxi*).
- KBIN-OC. 1920, IG27401: Golan, Israel. (Dissected specimen: MG058).
- KBIN-OC. 1921: spring in the Botanical Garden in Madrid (Spain) 40°25'N 3°43'W. Coll.: A. BALTANAS & L. AGUERA, 15-10-1995. (Dissected specimen: GR002).
- KBIN-OC. 1922: Degollada de Peraza in La Gomera (Spain) 28°08'N 17°14'W. Coll.: A. BALTANAS, 14-8-1990. (Dissected specimen: GR005).
- BALTANAS collection: Degollada de Peraza in La Gomera (Spain) 28°08'N 17°14'W. Coll.: A. BALTANAS, 14-8-1990. (Dissected specimens: Ref.264-265).
- BALTANAS collection: spring in the Botanical Garden in Madrid (Spain) 40°25'N 3°43'W. Coll.: A. BALTANAS & L. AGUERA, 15-10-1995. (Dissected specimen: GR004). (K. Martens 35).
- BALTANAS collection,: I.O.W. Bath (England). Coll.: D. HORNE, 14-10-1995 (Dissected specimen: GR001).
- ZMB 13155: St. Helena (Africa). Coll.: VAN HÖFFER. (Dissected specimen: MG138).

Herpetocypris lenta (= Herpetocypris brevicaudata)

- KBIN-OC.: type material: Parc S. Donat, large pond, near Louvain 50°53'N 4°42'E. Coll.: D.R. ROME, 26-08-1944 (IG15753).

Herpetocypris ehringsdorfensis (Pleistocene)

- MNIP 665/54 Ehringsdorf, Weimar (Germany) 50°59'N 11°20'E. Coll.: ZEISSLER, 24-05-1954.