

Original Article

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Binkhorstiidae, a new family of crabs (Decapoda, Brachyura, Retroplumoidea) from the Upper Cretaceous of the Netherlands and Belgium

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Abstract

In addition to the type species, *Binkhorstia ubaghsii*, which is fairly common in the upper part of the Nekum Member (Maastricht Formation) in the wider vicinity of Maastricht (the Netherlands) and *Binkhorstia euglypha*, which appears to be restricted to the overlying Meerssen Member of the same formation (uppermost Maastrichtian), a third member, *B. desaegheri* nov. sp., is recorded from the upper middle Santonian of the Campine area in north-east Belgium. The history of *Binkhorstia* is convoluted, serving as a prime example of how attempts to unravel the higher-level taxonomic position of late Mesozoic crabs may prove difficult. Over time, the genus has been referred to various families or subfamilies, either podotreme or putative eubrachyuran; here the new family Binkhorstiidae is placed in the superfamily Retroplumoidea. Binkhorstiids appear to have been a relatively short-lived endemic group that fell victim to Cretaceous–Paleogene (K/Pg) boundary perturbations.

Introduction

The brachyuran genus *Binkhorstia* Noetling, 1881 is known exclusively from the Upper Cretaceous of the south-east Netherlands and north-east Belgium (Figure 1). Until now, it comprised the type species, *Dromilites ubaghsii* van Binkhorst, 1857, occurring mainly in the upper Nekum Member (Maastricht Formation; upper Maastrichtian), and *Binkhorstia euglypha* Collins, Fraaije & Jagt, 1995, which appears to be restricted to the overlying Meerssen Member (Maastricht Formation; uppermost Maastrichtian) (see Fraaije, 2003, fig. 5). Here we add a third species, *B. desaegheri* nov. sp., from the upper middle Santonian of Houthalen (Campine area, north-east Belgium).

The history of *Binkhorstia* is convoluted, serving as a prime example of how attempts to unravel the higher-level taxonomic position of late Mesozoic crabs may prove difficult. Over time, the genus has been referred to various families or subfamilies, either podotreme or putative eubrachyuran, as follows:

- Cyclodorippidae, by Feldmann & Villamil (2002, p. 721);
- Necrocarcinidae, by Collins (2003, p. 85), Collins & Jakobsen (2004, p. 71) and Larghi (2004, p. 530);
- Torynommatidae, by Glaessner (1980, p. 181), De Grave et al. (2009, p. 29), Van Bakel et al., (2003, pp. 85–87) and Schweitzer et al., (2010, p. 78);
- Dorippidae, by Glaessner (1969, p. R492) and Quayle & Collins (1981, p. 738);
- Carcineretidae, by Wright & Collins (1972, p. 91), Collins et al., (1995, p. 199), Fraaije (1996, p. 271), Jagt et al., (2000, p. 40) (see also Wright, 1997, p. 138);
- Longosorbiidae, by Schweitzer & Feldmann (2011, p. 16).

However, more recently it has been recognised that *Binkhorstia* would warrant a family of its own (Schweitzer & Feldmann, 2011, p. 16, Guinot et al., 2013, p. 201). Members of this genus are characterised by a flattened, subsquare carapace, with undivided lateral margins, a wide thoracic sternum, a spatulate rostrum and reduced P5, positioned laterally to the first pleonal somite. We shall here examine the previous hypothesis put forward by Guinot et al., (2013, p. 201) that *Binkhorstia* might have affinities with members of the superfamily Retroplumoidea Gill, 1894,

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Figure 1. Schematic map of the Maastricht (Netherlands) and Campine (Belgium) areas, with localities (quarries, outcrops) that have yielded species of *Binkhorstia*, and stratigraphical ranges of *B. ubaghshii*, *B. euglypha* and *B. desaegheri* nov. sp.

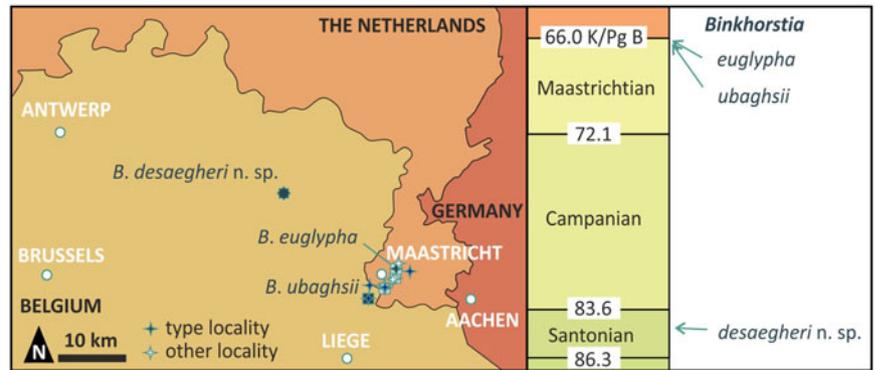
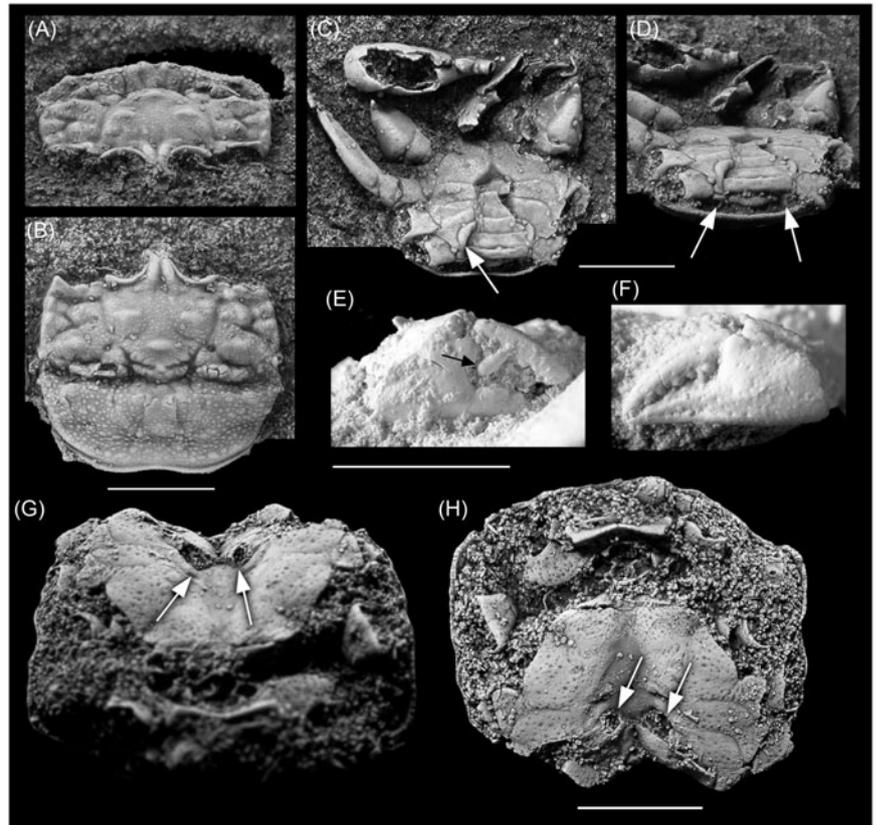


Figure 2. *Binkhorstia ubaghshii* (van Binkhorst, 1857): (A–D) male specimen (MAB 15928, leg. Robert Pieters) in oblique dorsal (A), dorsal (B), ventral (C) and oblique ventral (D) aspects, CBR-Romontbos quarry (Eben Emael, province of Liège, north-east Belgium), upper third of Nekum Member, Maastricht Formation (upper Maastrichtian), arrow in C indicates vertically oriented sternite 7, arrows in D indicate coxae of fifth pereopods; (E, F) right (major) and left (minor) cheliped, arrow indicates molariform crushing tooth; (G, H) female specimen (MAB15929, leg. Yvonne Coole) in oblique ventral, and ventral view, arrows indicate vulvae at extremity of suture (see text for details), CBR-Romontbos quarry (Eben Emael, province of Liège, north-east Belgium), upper third of Nekum Member, Maastricht Formation (upper Maastrichtian). All scale bars equal 5 mm.



erect a new family, Binkhorstiidae nov. and a new species, *B. desaegheri* nov. sp., and discuss its position within that superfamily.

The two late Maastrichtian species of *Binkhorstia* co-occur mainly with (in order of commonness) ghost shrimp, palaeocorystoids, raninoids, xanthoids and paguroids. The new late middle Santonian species is associated with the ghost shrimp *Mesostylus faujasi* (Desmarest, 1822) (see also Goolaerts & Mottequin, 2023, fig. 5B–D). *Binkhorstia* is known only from the study area and probably was endemic to it, being adapted to fairly fine-grained silty sands (Santonian) and biocalcarenic intra-reefal environments of the upper Maastrichtian of the south-east Netherlands and surrounding areas (Figure 1).

Material and methods

Binkhorstia ubaghshii is fairly common and numerous specimens of variable carapace sizes are housed in the MAB and NHMM collections, inclusive of a few corpses (Figure 2) (see Jagt et al., 2000; Van Bakel et al., 2003). The second species, *B. euglypha*, is much less common. Following the description of the type specimen (Figure 3C; see Collins et al., 1995), a handful of additional individuals has been brought to our attention. The single specimen of the new species, *B. desaegheri* nov. sp. (Figure 3B), is housed in the IRSNB collections; this was found amongst the material collected from bulk sampling during construction of colliery shafts.

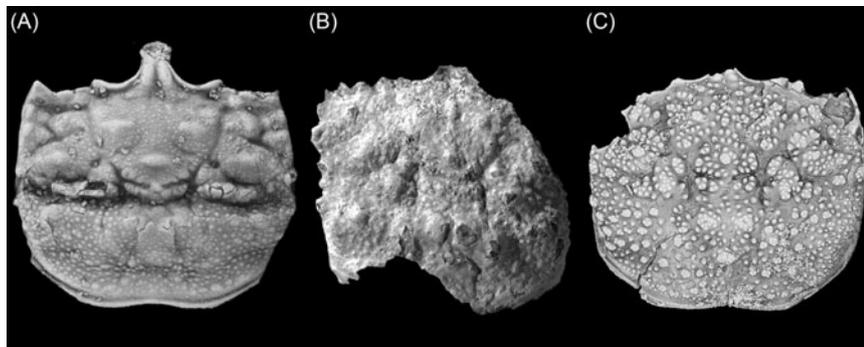


Figure 3. Carapaces (dorsal view) of *Binkhorstia* spp.: (A) *Binkhorstia ubaghsii*, for data see Figure 2; (B) *B. desaegheri* sp. nov., holotype (IRSNB 11512, shaft I of Houthalen colliery, eastern Campine Basin (north-east Belgium), depth 583–585 m below surface, Vaals Formation, either middle/upper part of Asdonk Member, or basal part of overlying Sonnisheide Member, upper middle Santonian); (C) *B. euglypha* Collins, Fraaye & Jagt, 1995, holotype (MAB15927), former Blom quarry (Berg en Terblijt, southern Limburg, the Netherlands), upper part of Meerssen Member, Maastricht Formation (uppermost Maastrichtian). Not to scale.

The following abbreviations are used in specimen descriptions: P1–P5, first to fifth pereopods (P1 as chelipeds; P2–P5 corresponding to ambulatory legs 1–4). Pleonal somites are numbered from 1 to 6. Thoracic sternal sutures are designated by the number of the two thoracic sternites that they involve and thus are numbered from 1/2 to 7/8.

Institutional abbreviations. **RBINS**, Royal Belgian Institute of Natural Sciences, Brussels, Belgium [note: **IRSNB** in collection registration]; **MAB**, Oertijdmuseum, Boxtel, the Netherlands; **MGSB**, Museo Geológico del Seminario de Barcelona, Barcelona, Catalonia, Spain; **MNHN**, Muséum National d'Histoire Naturelle Paris, France; **NHMM**, Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands; **NHMUK**, Natural History Museum, London, UK.

Comparative material

The following extinct and present-day retroplumoid taxa have been compared in detail with representatives of the genus *Binkhorstia*:

Extant

1. *Retropluma denticulata* Rathbun, 1932 – one male and two females (MNHN-IU 2022-3465, MNHN-IU-2022-3466), South China Sea, depths 99 m and 113 m (April 18, 1959);
2. *Retropluma notopus* (Alcock & Anderson, 1894) (type species of *Retropluma*) – one male (MNHN-IU-2022-3462 = MNHN-B29874), Fiji, Campagnes MUSORSTOM 10;
3. *Retropluma planiforma* Kensley, 1969 – two males (MNHN-IU-2022-3463 = MNHN-B7015), Madagascar, Campagne CREVETTIERE 1973 (Crosnier Collection);
4. *Retropluma plumosa* Tesch, 1918 – two females (MNHN-IU-2022-3460 = MNHN-B28866), Indonesia, KARUBAR Expedition 1991;
5. *Retropluma quadrata* de Saint Laurent, 1989 – male (holotype, MNHN-IU-2017-8034 = MNHN-B7009), Philippines, MUSORSTOM 1;
6. *Retropluma serenei* de Saint Laurent, 1989 – male (holotype, MNHN-IU-2017-8033 = MNHN-B19531), north-west Philippines, MUSORSTOM 3;
7. *Retropluma solomonensis* McLay, 2006 – male (holotype, MNHN-IU-2017-8024 = MNHN-B29870), Solomon Islands, SALOMON 1;
8. *Bathypluma forcifcula* de Saint Laurent, 1989 – male (holotype, MNHN-IU-2017-8040 = MNHN-B11229), Strait of Makassar, CORINDON 2;

9. *Bathypluma spinifer* de Saint Laurent, 1989 – male (holotype, MNHN-IU-2014-20496 = MNHN-B11226), Philippines, MUSORSTOM 2.

Fossil

1. *Costacopluma concava* Collins & Morris, 1975 – holotype (NHMUK In. 44642) and paratypes (NHMUK In. 44643–44648), Campanian–?Maastrichtian, south-east Nigeria; and NHMUK IC 1284, Cenomanian of Texas (see Collins et al., 2018);
2. *Gaudipluma bacamortensis* Artal, Van Bakel, Fraaije & Jagt, 2013 – holotype (MGSB75283) and paratypes (MGSB75284, 75285a, b, 75286a, b, MAB15918, 15919), Ypresian (Lower Eocene), Bacamorta, Huesca, Spain;
3. *Loerenthopluma danielae* Van Bakel, Artal, Fraaije & Jagt, 2010 – holotype (MAB15920) and twelve paratypes (MAB15921A–L), Ypresian (Lower Eocene), Egem, north-west Belgium;
4. *Retrocyopoda almelai* Via Boada, 1959 – holotype (MGSB 20123), Lutetian (Middle Eocene), Catalonia, Spain;
5. *Retropluma eocenica* Via Boada, 1959 – MGSB68417, upper Ilerdian (Lower Eocene), Bacamorta, Huesca, Spain); MGSB68420, middle Lutetian (Middle Eocene), Vilada, Catalonia, Spain; MGSB23738, middle Ilerdian (Lower Eocene), Terrades, Catalonia, Spain;
6. *Retropluma gallica* Artal, Van Bakel & Castillo, 2006 – holotype (MGSB68408), paratype (MGSB68409) and additional material (MGSB68410–13), Ilerdian (Lower Eocene), Fontcouverte, Corbières, southern France;
7. *Serrablopluma diminuta* Artal, Van Bakel, Fraaije & Jagt, 2013 – holotype (MGSB75287), paratypes (MGSB75289, MGSB75290a, b, MGSB78334a, b, MGSB78335a, b, c, MAB15922–15926), Priabonian (Upper Eocene), Yebra de Basa, Huesca, Spain.

Systematic palaeontology

Infraorder Brachyura Latreille, 1802

Section Eubrachyura de Saint Laurent, 1980

Superfamily Retroplumoidea Gill, 1894

Family Binkhorstiidae nov.

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Type, and sole, genus included. *Binkhorstia* Noetling, 1881.

Species included. In addition to the type species, *Dromilites ubaghsii* van Binkhorst, 1857, *B. euglypha* Collins, Fraaye & Jagt, 1995 and *B. desaegheri* nov. sp. (see below) (Figure 3).

Stratigraphical range. Late middle Santonian to latest Maastrichtian.

Palaeoenvironment. Sandy/silty and biocalcarenitic, shallow-water settings.

Diagnosis. Carapace small-sized, subrectangular to subsquare, widest at about one-third of total carapace length from front; flattened in both directions. Lateral margins weakly arched; anterolateral margins shorter than posterolateral margins. Carapace sides perpendicular to dorsal carapace surface, no linea brachyura visible. Posterior margin wide, slightly narrower than orbitofrontal margin, sinuous, axially concave, rimmed, bearing fine granules. Orbitofrontal width nearly equal to maximum carapace width; front narrow, with concave sides, longitudinally bilobed, distally conspicuously spatulate. Supraorbital margin with three short indentations, outer orbital corner developed as short triangular tooth. Infraorbital margin salient, long. Orbits deep, horizontal. Dorsal regions well-defined anteriorly may be with central tubercle. Cardiac grooves weak; anterior groove system complex, gastric grooves well defined. Cuticle surface entirely granular, granules may be clustered. Pterygostome narrow, inflated.

Chelae of male robust, heterochelous, heterodontous, palm short, fingers elongated, dactylus of major (right) chela with proximal crushing tooth; merus short, stout, globose. P2–P4 coxae in same plane, in ventral view progressively more closely spaced towards posterior. P2–P4 long, articles flattened. P5 coxae strongly reduced in size.

Thoracic sternum wide, subelliptical, flat; male sterno-pleonal cavity well-defined, narrow, deep, reaching halfway sternite 4; female sterno-pleonal cavity wider, shallow, subtriangular, reaching sternite 2. Episternites prominent, triangular. Sternite 5 widest, subhorizontal; sternite 6 narrower, slightly tilted towards posterior. Sternite 7 with exposed part conspicuously narrow, oriented obliquely; in females presence of distinct median (axial) line (i.e. medial line) (male disposition unknown). Sternite 8 completely covered by pleon in both sexes, likely distinctly reduced. Sternal sutures 4/5, 5/6 largely interrupted; suture 6/7 appearing to be complete (i.e. crossing thoracic sternum entirely). Pleon completely flexed under cephalothorax, all pleonal somites free. Sexual dimorphism markedly distinct: pleon wider in females, with narrow first somite. Pleonal holding structures not exposed in available material. Vulva at extremity of suture 5/6, suboval, large, closely spaced; aperture margin raised.

Genus *Binkhorstia* Noetling, 1881

Type species. *Dromilites ubaghsii* Van Binkhorst, 1857, by monotypy.

Binkhorstia desaegheri nov. sp.

Figs 3B

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Derivation of name. Named after Patrick De Saegher, RBINS volunteer, in recognition of his help in digitising the archives of the old 'palaeontology department', and in particular for his assistance in constructing a specimen-based inventory of Cretaceous invertebrates collected during shaft construction of collieries in the north-east Belgian Campine Basin, including the one at Houthalen that has yielded the type specimen of the new species.

Material. The holotype (maximum length 18 mm) (Figure 3B) is IRSNB 11512 (previously Invert-9780-0324), from a depth of 583–585 m below surface in shaft I of the Houthalen colliery, eastern Campine Basin, north-east Belgium (Figure 1). This specimen was initially registered on May 25, 1932 as IG (Inventaire

Général) 9780. It was collected from the Vaals Formation, either from the middle/upper part of the Asdonk Member, or the basal part of the overlying Sonnisheide Member. The boundary between both members lies between a depth of 585 and 571 m in shaft I at Houthalen (for further discussion, see Goolaerts & Mottequin, 2023). This interval can be dated as late middle Santonian (*Goniot euthis westfalicagranulata* belemnite Zone, *sensu germanico*). Associated ammonites include *Placenticeras polyopsis* (Dujardin, 1837), which allows substantiating the Santonian age (for more details, see Jagt et al., 1995; Goolaerts & Mottequin, 2023).

Description. Although the carapace is compressed at an oblique angle during fossilisation, the carapace is essentially similar in outline to that of *B. ubaghsii* and *B. euglypha* (Figure 3). Orbitofrontal width very wide, equalling maximum carapace width, with two short notches, dividing into three triangular lobes; front narrow, with concave sides, longitudinally bilobed, distally not preserved. Well-defined dorsal regions anteriorly with curved epi- and mesobranchial lobes and a mesogastric lobe with a very pronounced and elongated, forwardly protruding anterior process. Clear, somewhat depressed urogastric. Cardiac grooves weak. Large single tubercles on protogastric, mesogastric, hepatic, epibranchial, mesobranchial and metabranchial regions, largest and dual tubercle on the cardiac region.

Cuticle microstructure is entirely granular.

Comparison. *Binkhorstia desaegheri* nov. sp. Differs from *B. ubaghsii* and *B. euglypha* in having a longer and more pronounced mesogastric process which also continues more anteriorly. *Binkhorstia desaegheri* nov. sp. has also the most distinct tuberculose carapace (see Figure 3).

Discussion

Several Cretaceous crab genera present dorsal carapaces that are superficially similar to that of *Binkhorstia*, such as *Longusorbis* Richards, 1975, *Carcineretes* Withers, 1922 and *Ophthalmoplax* Rathbun, 1935. Spiridonov (2020, p. 144) noted for these genera that, 'In general, the carapace outline and symmetry/asymmetry patterns are characters of considerable taxonomic value at the genus or family level'. Similarities in orbitofrontal configuration are obvious: a narrow front, wide orbits, short supramarginal notches, similar supramarginal teeth, and a rather similar disposition of carapace grooves and regions. Rather than being a podotreme, as has often been thought, *Binkhorstia* is an eubrachyuran, clearly demonstrated by the vulvae preserved in one specimen before us, so that comparisons below will exclusively relate to eubrachyuran families.

The new family, Binkhorstiidae nov., is here assigned to the Retroplumoidea, based on a set of characters (Figures 2 and 3) that leads to a configuration known only in members of this superfamily, as follows: flattened, squarish to rectangular carapace; vertical anterolateral and posterolateral margins undefined from each other; angular lateral margin with perpendicular walls; wide orbits that occupy the entire frontal margin and are visible dorsally; thin, spatulate rostrum; P5 coxae conspicuously reduced, placed posteriorly and adjacent to the pleon (see Figure 2D); subequal chelipeds; flattened P2–P4; long pleon with all somites free; presence of a rainure in front of the sterno-pleonal cavity (i.e. in front of the telson) in which are lodged the extremities of the first gonopods in males and female pleopods; wide thoracic sternum, with long sutures; strongly reduced thoracic sternite 8, with exposed part so tiny that it is barely discernible.

The superfamily Retroplumoidea, revised by de Saint Laurent (1989) and until now considered to contain only a single family, the Retroplumidae (Martin & Davis, 2001; Števcic, 2005; Ng et al., 2008), composed of only two extant genera, *Retropluma* Gill, 1894 and *Bathypluma* de Saint Laurent, 1989, but involving a much higher number of extinct genera. It is considered an 'ancient', deeply rooted clade (Guinot et al., 2013, 2019), an assertion supported recently by genetic analyses (Wolfe et al., 2023) and supported by the Cretaceous occurrence of Retroplumidae (*Costacopluma* Collins & Morris, 1975; *Cristipluma* Bishop et al., 1983) and Binkhorstiidae fam. nov.

Several characters of the type species, *B. ubaghsii*, are fairly unique, notably: the heterochelous and heterodontous chelipeds with the presence of a molariform tooth on the larger chela (being indicative of a shell-breaking behaviour; see Schäfer, 1954; Van Bakel et al., 2003, figs 1.1, 1.2; Dietl & Vega, 2008, p. 292; Schweitzer & Feldmann, 2010), as well as the narrow, vertically oriented thoracic sternite 7 in the male (unknown in the female). These traits are not shared by any extant retroplumid (see de Saint Laurent, 1989) that normally have a long male pleon, with all somites free (3, 4 and 5 fused in extant retroplumids); the male pleon with somite 6 ridged and laterally expanded in its posterior part (corresponding to developed locking pleonal structures; see Guinot, 1979, fig. 30C; even present, yet less marked in females; see Guinot, 1979, fig. 30E; de Saint Laurent, 1989, figs 13, 15), and a wide thoracic sternum with exposed part of sternite 7 directed obliquely (Figure 2C). In extant retroplumid species, pleonal somites 3–5 are fused in adult males but free in females (de Saint Laurent, 1989, fig. 13), which is not the case in either *B. ubaghsii* or *B. desaegheri* nov. sp. In addition, extant retroplumids show a dorsal carapace with crests in species of *Retropluma* (de Saint Laurent, 1989, figs 2, 11, 12, 14), but this is much attenuated in *Bathypluma*. The vertically oriented thoracic sternite 7 may be considered a basal trait; it is also known in other basal eubranchyurans such as *Componocancer* Feldmann, Schweitzer & Green, 2008, *Eogeryon* Ossó, 2021, *Marocarcinus* Guinot, De Angeli & Garassino, 2008 and *Styracocarcinus* Schweitzer & Feldmann, 2012.

All these features support the erection of a new family, Binkhorstiidae nov., the third to be recognised within the Retroplumoidea. Details of in-depth comparisons between the new family and other eubranchyuran families are as follows:

1. *Binkhorstiidae* vs *Retroplumidae*

A diagnosis of the Retroplumidae was provided by for example, Davie et al., (2015: 1108) and Feldmann & Schweitzer (2018, p. 1).

Guinot et al., (2013, p. 201) stated that *Binkhorstia* could have affinities with the Retroplumoidea, based on 'the wide thoracic sternum, spatulate rostrum, flattened P2–P4, and P5 which are reduced and placed laterally to the first abdominal somite'. In fact, *Binkhorstia* shares several characters with the Retroplumidae, including small size, a dorsoventrally flattened body; subrectangular or subsquare carapace; sharp lateral margins; carapace with vertical flanks and long posterior margin; orbitofrontal margin usually nearly as wide as carapace; large orbits; narrow, deflected and spatulate front; flat thoracic sternum, sternite 8 covered by male pleon (sternite 8 hardly discernible in Retroplumidae, see Guinot et al., 2013, fig. 34B, D); long and flattened P2–P4; P5 coxae much more closely interspaced; at base of pleon, P5 coxae distinctly reduced (see Figure 2C, D); subcircular and large vulvae, at extremity of suture 5/6 (see fig. 6). In Retroplumidae, however, the

carapace regions or grooves are weakly defined (regions well marked, defined by a complex system of grooves in Binkhorstiidae nov.); usually three blunt to acute crests are present on the dorsal surface (absent in Binkhorstiidae nov.); the carapace cuticle is without dense granulation or tuberculation (present in Binkhorstiidae nov.); and the supraorbital margin is continuous, without notches or teeth (notches and teeth present in Binkhorstiidae nov.). Additionally, in Retroplumidae sternite 3 is short, horizontal, undivided (low triangular, with median depression in Binkhorstiidae nov.); sternite 4 bears a distinct, curved tooth (not visible in Binkhorstiidae nov.); sternites 5, 6 are horizontal, with rather parallel long sutures (curved, with more or less oblique sutures in Binkhorstiidae nov.); sternite 7 similar to preceding sternites (conspicuously narrow and oblique in *Binkhorstia*); episternites are small (robust in Binkhorstiidae nov.); a salient prominence on sternite 5 corresponds to the structure for pleonal holding, see Guinot & Bouchard, 1998, fig. 17B (absent in Binkhorstiidae nov.); pleonal somite 6 is typically modified by a marked lateral projection for pleonal holding, see Guinot & Bouchard, 1998, fig. 17A (normal, i.e. rectangular, in Binkhorstiidae nov.) and all sternal sutures are incomplete (suture 6/7 complete in females of Binkhorstiidae nov.; fig. 2H) (males unknown).

Fossil and extant retroplumid crabs (see Artal et al., 2013, pp. 348, 351, figs 2D, 4F) have a fairly well-developed vulva near the extremity of suture 5/6 (Guinot, 1979, fig. 30E; de Saint Laurent, 1989, fig. 5); Binkhorstiidae nov. has conspicuously large apertures (Figure 2G, H). Additionally, in extant retroplumids the chelipeds are flattened, with slender fingers which lack shell-breaking structures. These additional differences warrant exclusion of *Binkhorstia* from the Retroplumidae. However, the numerous similarities allow *Binkhorstia* to be accommodated within the Retroplumoidea, assigned to its own family.

Several extinct retroplumid crabs have been described, in particular from the Eocene, some with a well-preserved sternum. The monotypical, small-sized *Serrablopluma* Artal, Van Bakel, Fraaije & Jagt, 2013, from the upper Eocene (Priabonian) of Huesca (north-east Spain), shows a typical retroplumid sternum (see Artal et al., 2023, figs 1, 2) with a subtriangular (narrow anterior) sternite 4, a normal (wide, developed) sternite 7, and a short, rather wide sternite 8 (Artal et al., 2023, fig. 2d), unlike the configuration in Binkhorstiidae nov. In *Serrablopluma* the pleonal somites have horizontal crests, the episternites being of normal development (large in *Binkhorstia*).

The large-sized and distinctly ornamented *Gaudipluma* Artal, Van Bakel, Fraaije & Jagt, 2013 (see Artal et al., 2013, Figs 3, 4) shows a characteristic thoracic sternum with oblique suture 4/5, a rather narrow female pleon, a distinct median line up to the level of suture 5/6, a conspicuously large and wide sternite 7, a sternite 8 that is the only small, inclined and subvertical sternite, and virtually absent episternites. In all these characters, *Gaudipluma* differs from Binkhorstiidae nov. In *Gaudipluma* the sternites 3, 4 are trapezoidal, and the anterior sternite 4 is wide, which is closer to *Binkhorstia* than to other retroplumids.

Retrocypoda Vía Boada, 1959 is a retroplumoid known from a single species, *R. almelai* Vía Boada, 1959, widely distributed in northern Spain, Italy and Iran (see de Saint Laurent, 1989, pl. 7A–D; Khodaverdi Hassan-vand et al., 2016), with an unpublished record from Hungary (M. Hyžný, pers. comm., May 2024). It is characterised by a carapace with subhorizontal and oblique sinuous crests (see Khodaverdi Hassan-vand et al., 2016, fig. 4), pleonal somites and wide thoracic sternites with strongly

developed horizontal crests, and, as befits the family, large and robust chelipeds (Ferratges, 2017, fig. 30C, D). These characters do not match those of the Binkhorstiidae nov.

Loerenthopluma Beschin, Busulini, De Angeli & Tessier, 1996, known from two species from the Eocene–Oligocene of Belgium, Italy and Hungary (see Beschin et al., 1996; Hyžný & Müller, 2010; Van Bakel et al., 2010), was ‘considered to be closely related to *Retropluma*’ (Van Bakel et al., 2010, p. 46). Indeed, the thoracic sternum and pleon of *Loerenthopluma* are closely similar to those of *Retropluma* (compare Van Bakel et al., 2010, fig. 1, and Beschin et al., 1996, fig. 4.3).

Several fossil species of *Retropluma* are known. *Retropluma minuta* Gašparič, Hyžný, Jovanović, Čorić & Vrabac, 2019, from the middle Miocene of Slovenia, is small sized, has a squarish carapace and slender chelipeds; pleonal segment 6 is widened for the pleonal locking system, and somites 3–5 are apparently fused. The genus appears to have originated in the early Eocene. *Retropluma eocenica* is first known from upper Ilerdian (lower Eocene) deposits in Spain; *R. gallica* from the Ilerdian of Corbières, southern France.

As far as the Cretaceous is concerned, *Costacopluma* is known from the Coniacian and survived the K/Pg event into the Eocene; it is widespread from Nigeria and Senegal to Greenland, from the USA to Brazil and Argentina (see Hyžný et al., 2015, table 1; fig. 9). *Costacopluma* is characterised by a subovate carapace outline, with distinct, inflated, transverse crests on the dorsal surface, devoid of distinct tubercles as in *Binkhorstia*. The thoracic sternites are wide and show acute oblique ridges (flat in *Binkhorstia*), the episternites are weakly developed (conspicuously large in *Binkhorstia*), and the vulvae on sternite 6 are smaller (compare Armstrong et al., 2009, fig. 5.17).

In summary, characters shared by the families Retroplumidae and Binkhorstiidae nov. are sternite 8 very reduced, not dorsally visible or hardly discernible; a similar rainure in front of the sternopleonal cavity (in which extremities of the first gonopods in males and of pleopods in females are lodged); the vulva at the extremity of suture in Binkhorstiidae nov. (fig. 6) as in extant retroplumids (Guinot, 1979, fig. 30E; de Saint Laurent, 1989, fig. 5; Guinot et al., 2013, fig. 5D).

Binkhorstiidae vs Longusorbiidae

Schweitzer & Feldmann (2011, p. 16) provisionally placed *Binkhorstia* in the Longusorbiidae Karasawa, Schweitzer & Feldmann, 2008, a family erected to contain a single genus, *Longusorbis*, which includes three species (see Schweitzer et al., 2010, p. 106). Schweitzer & Feldmann (2011, p. 16) listed the similarities between *Binkhorstia* and Longusorbiidae, noting that, ‘a front that can be interpreted as lying between the interior-most orbital notches; a long, spatulate rostrum with a strongly downturned tip; very broad, sinuous, notched orbits; a fronto-orbital width that is about equal to the maximum carapace width; short gastric regions and long branchial regions; sternites 1 and 2 fused; sternal suture 3/4 developed as a notch laterally; sternite 4 long; sternal sutures 4/5 and 5/6 not parallel; sternite 8 not visible in ventral view; and all male abdominal somites free’. The same authors also drew attention to a number of significant differences: ‘The male abdomen does not seem to fill the entire space between the coxae of the fifth pereopods in *Binkhorstia*, and the overall carapace shape and ornamentation is different in *Binkhorstia* than in *Longusorbis*’. In addition to these differences, we note that:

- *Longusorbis* has a subtrapezoidal carapace (subrectangular in *Binkhorstia*);
- *Longusorbis* lacks a shell-breaking tooth on the major chela dactylus (present in *Binkhorstia*);
- *Longusorbis* has a normal P5 (strongly reduced in *Binkhorstia*);
- *Longusorbis* has a normal thoracic sternite 7 (narrow and obliquely directed in *Binkhorstia*).

Binkhorstia cannot be included in the Longusorbiidae on the basis of the differences outlined above. Longusorbiids are currently included in the superfamily Portunoidea (Spiridonov, 2020), a position is in need of further testing.

Binkhorstiidae vs Dorippoidea

Glaessner (1969, p. R492) assigned *Binkhorstia* to the Dorippidae H. Milne Edwards, 1837, followed by Quayle & Collins (1981, p. 738). The squarish carapace with well-defined anterior regions of *B. ubaghsii* (only with an ornament of granules and tubercles in *B. euglypha* and *B. desaegheri* nov. sp.) does not resemble the ovate dorippoid carapace that has special grooves, often delineating a human-like face. Several other characters exclude Binkhorstiidae nov. from the Dorippoidea (see Guinot, 2023, p. 370), such as:

- P4 and P5 reduced in Dorippoidea (only P5 in Binkhorstiidae nov.);
- posterolateral margin not well defined and with perpendicular edge in Dorippoidea (well-defined, perpendicular in Binkhorstiidae nov.);
- Dorippoidea without a shell-breaking tooth on major chela dactylus (present in Binkhorstiidae nov.);
- pleon curved, with first somites dorsally exposed, in prolongation with carapace in Dorippoidea (entirely flexed, held under body in Binkhorstiidae nov.);
- rostrum bidentate, with more or less concave axial notch in Dorippoidea (narrow, spatulate in Binkhorstiidae nov.);
- thoracic sternum strongly flexed posteriorly in Dorippoidea (flat in Binkhorstiidae nov.); thoracic suture 5/6 strongly concave (normal in Binkhorstiidae nov.);
- sternite 8 with exposed part dorsally visible (see Guinot, 2023, fig. 8B, C) (strongly reduced in Binkhorstiidae nov.).

The extinct dorippoid family Telamonocarcinidae Larghi, 2004, originally erected as a subfamily, but elevated to family status by Guinot et al., (2013, p. 306), and recently re-considered (Luque, 2015; Van Bakel et al., 2023), now contains the genera *Eodorippe* Glaessner, 1980 and *Telamonocarcinus* Larghi, 2004 (type genus). Telamonocarcinids differ from *Binkhorstia*, in addition to differences with the Dorippoidea listed above, in lacking orbital fissures and spines and in having strong outer orbital spines.

Binkhorstiidae vs Carcineretidae

On several occasions, *Binkhorstia* has been placed in the Carcineretidae Beurlen, 1930, for instance by Wright & Collins (1972, p. 91), Collins et al., (1995, p. 199), Fraaye (1996b, p. 271) and Jagt et al., (2000, p. 40), in view of an overall similar appearance: squarish, flat carapace with wide orbits, and regions ornamented with tubercles. At the time, the Carcineretidae also contained *Ophthalmoplax*, which later was transferred to the Portunoidea (Polybiniidae; see Schweitzer et al., 2007, p. 22) and

subsequently to the portunoid family Macropipidae by Karasawa et al., (2008, p. 100). Ossó-Morales et al., (2010, p. 219) provisionally concurred with that placement. The type genus *Carcineretes* has strongly developed P5 with flattened distal elements, transformed into highly specialised swimming tools (see Jagt et al., 2015, fig. 71-15.2C), very unlike the conspicuously reduced P5 of *Binkhorstia*. The front in *Carcineretes* is rather wide, downturned but not spatulate (*vs* very narrow and spatulate in *Binkhorstiidae* nov.). In *Carcineretes*, the male pleonal somites 3–5 are fused, and the male pleonal somites 1 and 2 are in contact with the P5 coxae, unlike the disposition in the new family. Thoracic sternite 7 is not conspicuously narrow and vertical, but similar to the preceding thoracic sternites. The lower margin of the chelae is sharply rimmed, while that of *Binkhorstia* is rounded. The dentation, including a shell-crushing molar, is otherwise similar. These differences exclude *Binkhorstia* from the Carcineretidae.

Binkhorstiidae vs *Archaeopidae*

The monotypical family Archaeopidae Karasawa, Kishimoto, Ohara & Ando, 2019, recently established to accommodate the genus *Archaeopus* Rathbun, 1908 (type species, by monotypy, *A. antennatus* Rathbun, 1908), contains eight species of Late Cretaceous to Eocene age from the Pacific coast of North America and Japan (Nyborg et al., 2019). This had previously been included in the Retroplumidae, but this status was considered doubtful (see de Saint Laurent, 1989; McLay, 2006; Guinot et al., 2013). The genus was described at length by Guinot et al., (2013, p. 140), and species were revised and added by Nyborg et al., (2019, p. 48). It was distinguished from the Retroplumidae on the basis of carapace, sternal and pleonal characters (Karasawa et al., 2019).

The female thoracic sternum of the type species, *A. antennatus*, shows a conspicuously large, elongate pleonal somite 6 (see Nyborg et al., 2019, fig. 5B). The thoracic sternum of *Archaeopus* is subcircular, wide, with oblique thoracic sternites, which are weakly ridged. Sternite 8 is covered by the male pleon, P5 appears to be strongly reduced. The carapace lateral margins bear several blunt spines and nodes, more or less comparable with *Binkhorstia*.

Members of *Binkhorstiidae* nov. appear to be similar in dorsal aspect to Archaeopidae, sharing the subsquare carapace outline, the undifferentiated, subvertical and sharp-edged lateral margins, the horizontal orbital margin that is practically as wide as the carapace, the narrow and spatulate rostrum (at least in some members of the Archaeopidae; see Nyborg et al., 2019, figs 7, 8) and the reduced P5. However, there are several significant differences between the Archaeopidae and *Binkhorstiidae* nov., including:

- Archaeopids have inflated carapace regions, with horizontally elongated nodes on the dorsal carapace (weakly vaulted regions, only in gastric area with central tubercle in *Binkhorstiidae* nov.);
- In archaeopids, the lowest point of the cervical groove, thus the gastric pits, are below carapace mid-length (gastric pits more anteriorly situated, above carapace mid-length in *Binkhorstiidae* nov.);
- Archaeopids have very wide protogastric regions (narrow in *Binkhorstiidae* nov.);
- In archaeopids, thoracic sternites 3 and 4 are clearly distinguished by a prominent, oblique groove (only a weak lateral incision in *Binkhorstiidae* nov.);

- Female sternoabdominal depression stops on sternite 4 in Archaeopidae (see Nyborg et al., 2019, fig. 5B), but continues up to sternite 2 in *Binkhorstiidae* nov.;
- Male sternite 7 is normal in Archaeopidae (arched, narrow and oriented obliquely in *Binkhorstiidae* nov.);
- Chelae in archaeopids are robust, with long, pointed fingers without shell-crushing molar (small, more compact and with shell-crushing molar in *Binkhorstiidae* nov.).

Binkhorstia cannot be included in the Archaeopidae because of the differences outlined above. Both families could be basal retroplumoids.

Binkhorstiidae vs *Lithophylacidae*

The monotypical Lithophylacidae Van Straelen, 1936, occurring in the Cenomanian (Upper Cretaceous) of France (see Guinot & Breton, 2006), shows some similarities to *Binkhorstia* in that P5 is strongly reduced, the orbital margin occupies the maximum carapace width and there is a narrow, spatulate rostrum. Lithophylacids were considered as basal Portunoidea by Karasawa et al., (2008, p. 84), and regarded as closely related to the Icriocarcinidae (Phillips et al., 2013, p. 151; Teodori et al., 2013, p. 73). *Lithophylax* differs from *Binkhorstia* in numerous ways; most significantly, *Lithophylax* has:

- transverse ridges on the carapace;
- a carapace that is wider than long;
- strongly divergent lateral margins;
- no orbital notches and teeth;
- the female sterno-pleonal depression does not reach sternite 3 (crossing sternite 3 in *Binkhorstia*);
- thoracic sternite 7 is not conspicuously narrow and directed obliquely directed, but normal, as preceding sternites;
- there is no shell-crushing tooth on the major chela dactylus;
- there is a stridulating apparatus in *Lithophylax*, absent in *Binkhorstia*.

Binkhorstiidae vs *Ophthalmoplax*

Ophthalmoplax, previously included in the portunoid family Macropipidae (see Karasawa et al., 2008, p. 100; Ossó-Morales et al., 2010, p. 215; Schweitzer et al., 2010, p. 107), currently included in the portunoid family Carcinidae (Polybiinae) (Feldmann et al., 2018: 580), presents a squarish carapace with wide orbits, a sinuous orbital margin divided by short notches, a relatively well-marked gastrohepatic groove, and discontinuous horizontal crests [i.e. widened tubercles] in dorsal regions. However, the rostrum is wide, with four blunt nodes in two different planes and P5 is well-developed, flattened and paddle-like (Schweitzer et al., 2007, p. 18, table 1; Vega et al., 2013, fig. 3.4). Ossó-Morales et al., (2010, p. 219) mentioned that *Ophthalmoplax* might warrant its own subfamily.

Binkhorstiidae vs *Palicidae*

McLay (2006: 375) opined that some of the fossils placed in the Retroplumidae probably belong rather to the Palicidae Bouvier, 1898. Palicids have a subquadrate to rounded carapace outline, granular carapace surface, a sharp lateral margin, and P5 strongly reduced; these characters are shared with *Binkhorstiidae* fam. nov. The rostrum of Palicidae typically is wide, with multiple spines or lobes; a different morphology as in *Binkhorstiidae* fam. nov. or any

other Retroplumoidea. The P5 coxae are placed wide apart in Palicidae, unlike the narrow placement in Binkhorstiidae fam. nov. Also, the female thoracic sternum of Palicidae shows a distinctive configuration, with anterior advancement of sternites (Guinot *et al.*, 2013: 47) and the vulvae (see Guinot, 1979: fig. 31), which is unlike the disposition in *Binkhorstia*.

Conclusions

Members of the family Binkhorstiidae nov. are known exclusively from Santonian and upper Maastrichtian strata in the extended type area of the Maastrichtian Stage (south-east Netherlands and north-east Belgium). The groups appear to have been endemic to the area, ranging from the upper middle Santonian (siliciclastics) to uppermost Maastrichtian (carbonates). The history of *Binkhorstia* is a turbulent one; its higher-level taxonomic position has changed considerably over time, having been assigned to various families or subfamilies, either podotreme or putative eubrachyuran. Here we place Binkhorstiidae nov. in the superfamily Retroplumoidea, following a detailed comparison with the families to which *Binkhorstia* had previously been referred.

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References

- Acock, A. & Anderson, A.R.**, 1894. List of the shore and shallow-water Brachyura collected during the season 1893-1894. Natural History notes from H.M. Indian Marine Survey Steamer «Investigator», Commander C.F. Oldham, R.N., commanding. Series n. No. 17. Journal of the Asiatic Society of Bengal **63**, 2/4: 197–209.
- Armstrong, A., Nyborg, T., Bishop, G. A., A., Ossó-Morales, & Vega, F.J.**, 2009. Decapod crustaceans from the Paleocene of Central Texas, USA. Revista Mexicana de Ciencias Geológicas **26**(3): 745–763
- Artal, P., Van Bakel, B.W.M. & Castillo, J.**, 2006. *Retropluma*. Gill, 1894 (Crustacea, Decapoda) from the Eocene of the eastern Pyrenees (Spain, France). Cainozoic Research **5**: 63–69
- Artal, P., Van Bakel, B.W.M., Fraaije, R.H.B., & Jagt, J.W.M.**, 2013. New retroplumid crabs (Crustacea, Brachyura, Retroplumidae Gill, 1894) from the Eocene of Huesca (Aragón, Spain). Zootaxa **3652**: 343–352
- Beschin, C., Busulinia, A., De Angeli, & Tessier, G.**, 1996. Retroplumoidea (Crustacea, Brachyura) nel Terciario del Vicentino (Italia settentrionale). Lavori Società Veneziana di Scienze Naturali **21**: 83–102
- Beurlen, K.**, 1930. Vergleichende Stammesgeschichte. Grundlagen, Methoden, Probleme unter besonderer Berücksichtigung der höheren Krebse. Fortschritte in der Geologie und Paläontologie **8**: 317–586
- Binkhorst, J.T. van**, 1857. Neue Krebse aus der Maestrichter Tuffkreide. In: Verhandlungen des naturhistorischen Vereins in preußisch Rheinland und Westfalen 14-2. vol. **14**, 107–110, pls 1, 2 [5, 6]
- Bishop, G.A.**, 1983. Fossil decapod Crustacea from the Late Cretaceous Coon Creek Formation, Union County, Mississippi. Journal of Crustacean Biology **3**(3): 417–430.
- Collins, J.S.H.**, 2003. A taxonomic review of British decapod Crustacea. Bulletin of the Mizunami Fossil Museum **29**(for 2002): 81–92
- Collins, J.S.H., Fraaye, R. H. B. & Jagt, J.W.M.**, 1995. Late Cretaceous anomurans and brachyurans from the Maastrichtian type area. Acta Palaeontologica Polonica **40**: 165–210
- Collins, J.S.H. & Morris, S.F.**, 1975. A new crab, *Costacopluma concava*, from the Upper Cretaceous of Nigeria. Palaeontology **18**: 823–829
- Collins, J.S.H., Garvie, C. L. & Mellish, C.J.T.**, 2018. *Costacopluma concava*. Collins and Morris, 1975 (Decapoda, Brachyura) from the Woodbine Formation (Cenomanian) of Texas, USA. Cretaceous Research **87**: 145–149. DOI: [10.1016/j.cretres.2017.08.010](https://doi.org/10.1016/j.cretres.2017.08.010).
- Collins, J.S.H. & Jakobsen, S.L.**, 2004. New crabs (Crustacea, Decapoda) from the Eocene (Ypresian/Lutetian) Lillebælt Clay Formation of Jutland, Denmark. Bulletin of the Mizunami Fossil Museum **30**(for 2003): 63–96
- Davie, P.J.F., Guinot, D. & Ng, P.K.L.**, 2015. Systematics and classification of Brachyura. In: Castro P., Davie P. J. F., Guinot D., Schram F. & Von Vaupel Klein C. (eds): Treatise on Zoology – Anatomy, Taxonomy, Biology – The Crustacea, complementary to the volumes translated from the French of the Traité de Zoologie, 9(C) (I), Decapoda: Brachyura (Part 2)
- De Grave, S., Pentcheff, N.D., Ahnyong, S.T., Chan, T.-Y., Crandall, K.A., Dworschak, P.C., Felder, D.L., Feldmann, R.M., Fransen, C.H.J.M., Goulding, L.Y.D., Lemaitre, R., Low, M.E.Y., Martin, J.W., Ng, P.K.L., Schweitzer, C.E., Tan, S.H., D., Tshudy, & Wetzer, R.**, 2009. A classification of living and fossil genera of decapod crustaceans. The Raffles Bulletin of Zoology **(21)**: 1–109
- Desmarest, A.-G.**, 1822. Histoire naturelle des crustacés fossiles, sous les rapports zoologique et géologiques. Les crustacés proprement dits, vii + 184 pp., 11 pls. L.T. Cellot/F.G. Levrault, Paris.
- Dieth, G. & Vega, F.J.**, 2008. Specialized shell-breaking crab claws in Cretaceous seas. Biology Letters **4**(3): 290–293.
- Dujardin, F.**, 1837. Mémoire sur les couches du sol en Touraine et description des coquilles de la craie et des faluns. Mémoires de la Société géologique de France **2**: 211–311, pls 15-21
- Feldmann, R.M. & Schweitzer, C.E.**, 2018. Part R, Revised, Volume 1, Chapter 8T1: Systematic Descriptions: Superfamily Retroplumoidea Gill, 1894. Treatise Online **106**: 1–6. DOI: [10.17161/to.v010.7604](https://doi.org/10.17161/to.v010.7604).
- Feldmann, R.M., Schweitzer, C.E., Goedert, J.L.**, 2018. Complex taphonomic and depositional history of a new species of Carcinidae (Decapoda: Brachyura: Portunoidea) from Washington state, USA. Journal of Crustacean Biology **38**(5): 579–585. DOI: [10.1093/jcbiol/ruy066](https://doi.org/10.1093/jcbiol/ruy066).
- Feldmann, R.M., Schweitzer, C.E., Green, R.M.**, 2008. Unusual Albian (Early Cretaceous) Brachyura (Homoloidea: Componocancroidea new superfamily) from Montana and Wyoming, U.S.A. Journal of Crustacean Biology **28**(3): 502–509.
- Feldmann, R.M. & Villamil, T.**, 2002. A new carcineretid crab (Upper Turonian, Cretaceous) of Colombia. Journal of Paleontology **76**(4): 718–724.
- Ferratges, F.A.**, 2017. Los crustáceos fósiles de las cuenca surpirenaicas. Cuadernos de Paleontología Aragonesa **8**: 1–100.
- Fraaije, R.H.B.**, 2003. Evolution of reef-associated decapod crustaceans through time, with particular reference to the Maastrichtian type area. Contributions to Zoology **72**(2-3): 119–130.
- Fraaye, R.H.B.**, 1996. Late Cretaceous swimming crabs: radiation, migration, competition, and extinction. Acta Geologica Polonica **46**(3-4): 269–278, pl. 1
- Gašparič, R., Hyžný, Múš, Jovanović, G., Čorić, S., Vrabac, S.**, 2019. Middle Miocene decapod crustacean assemblage from the Tuzla Basin (Tušanj, Bosnia and Herzegovina), with a description of two new species and comparison with coeval faunas from Slovenia. Palaeontologia Electronica **22**(1.9A): 1–21. DOI: [10.26879/894](https://doi.org/10.26879/894).
- Gill, T.**, 1894. A new Bassalian type of crabs. American Naturalist **28**(336): 1043–1045.
- Glaessner, M.F.**, 1969. Decapoda. In: Moore R.C. (ed): Treatise on Invertebrate Paleontology, Part R. vol. **4**, The Geological Society of America, Boulder/The University of Kansas Press (Lawrence): R400–R533–R626–R628.
- Glaessner, M.F.**, 1980. New Cretaceous and Tertiary crabs (Crustacea: Brachyura) from Australia and New Zealand. Transactions of the Royal Society of South Australia **104**: 171–192.
- Goolaearts, S. & Mottequin, B.**, 2023. A Santonian record of the nautilid cephalopod *Angulithes westphalicus* (Schlüter, 1872) from the subsurface of the Campine, north-east Belgium, with comments on regional lithostratigraphic problems. Geologica Belgica **26**(1-2): 101–113. DOI: [10.20341/gb.2023.007](https://doi.org/10.20341/gb.2023.007).
- Guinot, D.**, 1979. Données nouvelles sur la morphologie, la phylogénèse et la taxonomie des Crustacés Décapodes Brachyours. Mémoires du Muséum national d'Histoire naturelle, A. Zoologie **112**: 1–354.
- Guinot, D.**, 2023. A new subfamily classification of the highly diversified Dorippidae H. Milne Edwards, 1837 (Crustacea, Brachyura, Dorippoidea), using morphological, molecular and palaeontological data, with

- special emphasis on its unique female reproductive system. *Zoosystema* 45(9): 225–372.
- Guinot, D. & Bouchard, J.M.**, 1998. Evolution of the abdominal holding systems of brachyuran crabs (Crustacea, Decapoda, Brachyura). *Zoosystema* 20(4): 613–694.
- Guinot, D. & Breton, G.**, 2006. Lithophylax trigeri. A. Milne-Edwards & Brocchi, 1879 from the French Cretaceous (Cenomanian) and placement of the family Lithophylacidae Van Straelen, 1936 (Crustacea, Decapoda, Brachyura). *Geodiversitas* 28: 591–633.
- Guinot, Dèle, Carbot-Chanona, G. Vega, FJ**, 2019. Archaeochiapasidae n. fam., a new early Cenomanian brachyuran family from Chiapas, Mexico, new insights on Lecythocaridae Schweitzer & Feldmann, 2009, and phylogenetic implications (Crustacea, Decapoda, Brachyura, Eubrachyura). *Geodiversitas* 41(1): 285–322. DOI: [10.5252/geodiversitas2019v41a7](https://doi.org/10.5252/geodiversitas2019v41a7).
- Guinot, D., A., De Angeli & Garassino, A.**, 2008. Marocarcinidae, a new eubrachyuran family, and *Marocarcinus pasinii* n. gen. n. sp. from the Upper Cretaceous (Cenomanian-Turonian) of Gara Sbaa, southeastern Morocco (Crustacea, Decapoda, Brachyura). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 149(1): 25–36.
- Guinot, D., M., Tavares & Castro, P.**, 2013. Significance of the sexual openings and supplementary structures on the phylogeny of brachyuran crabs (Crustacea, Decapoda, Brachyura), with new nomina for higher-ranked podotreme taxa. *Zootaxa* 3665(1): 1–414.
- Hyžný, M., Müller, P.M.**, 2010. Loerenthopluma Beschin, Busulini, De Angeli & Tessier, 1996 (Decapoda, Brachyura, Retroplumidae) from the Oligocene of Hungary. *Atti della Società italiana di Scienze naturali e Museo civico di Storia naturale di Milano* 151(II): 123–134.
- Hyžný, M., Perrier, V. Robin, N., J.E., Martin, & Sarr, R.**, 2015. *Costacopluma* (Decapoda: Brachyura: Retroplumidae) from the Maastrichtian and Paleocene of Senegal: a survivor of K/Pg events. *Cretaceous Research* 57: 142–156. DOI: [10.1016/j.cretres.2015.08.010](https://doi.org/10.1016/j.cretres.2015.08.010).
- Jagt, J.W.M., Fraaye R.H.B., & Van Bakel, B.W.M.**, 2000. Late Cretaceous decapod crustacean faunas of northeast Belgium and the southeast Netherlands. *In: 1st Workshop on Mesozoic and Tertiary decapod crustaceans. Studi i Ricerche, Associazione Amici del Museo, Museo civico G. Zannato. vol. 7, Montecchio Maggiore (Vicenza):* 37–42
- Jagt, J.W.M., Kennedy, W. J., Burnett, J.A., Christensen W.K., & Dhondt, A. V.** 1995. Santonian macrofauna and nannofossils from northeast Belgium. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, 65, p. 127–137, pl. 1.
- Jagt, J.W.M., Van Bakel, B.W.M., Guinot, D., R.H.B., Fraaije, & Artal, P.**, 2015. Fossil Brachyura. *In: Castro P. Davie, Guinot P.J.F., Schram D. & Von Vaupel Klein C. (eds): Treatise on Zoology—Anatomy, Taxonomy, Biology—The Crustacea, complementary to the volumes translated from the French of the Traité de Zoologie, 9(C) (I), Decapoda: Brachyura (Part 1). E.J. Brill (Leiden):* 847–920.
- Karasawa, H., Schweitzer, C.E. & Feldmann, R.M.**, 2008. Revision of Portunoidea Rafinesque, 1815 (Decapoda: Brachyura) with emphasis on the fossil genera and families. *Journal of Crustacean Biology* 28(1): 82–127.
- Karasawa, H., Kishimoto, S.M., Ohara, Ando, Y.**, 2019. Late Cretaceous Decapoda from the Izumi Group of Japan, with descriptions of two new genera and one new species of Axiidea and one new family of Brachyura. *Bulletin of the Mizunami Fossil Museum* 45: 43–85.
- Kensley, B.**, 1969. Decapod Crustacea from the south-west Indian Ocean. *Annals of the South African Museum* 52: 149–181
- Khodaverdi Hassan-vand, M., Bahrami, A.Yazdi, M., Ossó, À., Safari, A., Martínez, J.L., & Vega, F.J.**, 2016. Occurrence of *Retrocypoda almelai* Via Boada, 1959 (Decapoda: Retroplumidae) in the Eocene of Central Iran. *Paleontología Mexicana* 5(1): 21–31.
- Larghi, C.**, 2004. Brachyuran decapod Crustacea from the Upper Cretaceous of Lebanon. *Journal of Paleontology* 78(3): 528–541.
- Latreille, P.A.**, 1802–1803. Histoire naturelle, générale et particulière, des Crustacés et des Insectes. Ouvrage faisant suite aux oeuvres de Leclerc de Buffon, et partie du Cours complet d'Histoire naturelle rédigé par C.S. Sonnini, membre de plusieurs Sociétés savantes 3. F. Dufart (Paris): xii + 467 pp., <https://doi.org/10.5962/bhl.title.15764>.
- Luque, J.**, 2015. The oldest higher true crabs (Crustacea: Decapoda: Brachyura): insights from the Early Cretaceous of the Americas. *Palaeontology* 58(2): 251–263. DOI: [10.1111/pala.12135](https://doi.org/10.1111/pala.12135).
- Martin, J.W. & Davis, G.E.**, 2001. An updated classification of the Recent Crustacea. *Natural History Museum of Los Angeles County, Contributions in Science* 39: 1–124.
- McLay, C.L.**, 2006. Retroplumidae (Crustacea, Decapoda) from the Indo-Malayan archipelago (Indonesia, Philippines) and the Melanesian arc islands (Solomon Islands, Fiji and New Caledonia), and paleogeographical comments. *In: Richer de Forges B. & Justine J.-L. (eds): Tropical deep-sea benthos, volume 24. Mémoires du Muséum national d'Histoire naturelle Paris* 193, 375–391.
- Milne Edwards, H.**, 1834–1837. Histoire naturelle des Crustacés comprenant l'anatomie, la physiologie et la classification de ces animaux 1: xxxv + 468 pp.; 2: 531 + 32 pp. Librairie encyclopédique de Roret (Paris).
- Ng, P.K.L., Guinot D. & Davie, P.J.F.**, 2008. Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *The Raffles Bulletin of Zoology Supplement* 17: 1–286.
- Noetting, F.**, 1881. Ueber einige Brachyuren aus dem Senon von Mastricht [sic] und dem Tertiär Norddeutschlands. *Zeitschrift der deutschen geologischen Gesellschaft* 33: 357–371, pl. 20
- Nyborg, T., McLachlan, S. M.S., Garassino, A., Vega, F. J., Phillippe, S. C., Champagne, D. E.**, 2019. New and revised species of *Archaeopus* Rathbun, 1908 (Decapoda: Brachyura: Retroplumidae) from the eastern Pacific. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 292(1): 25–56. DOI: [10.1127/njgpa/2019/0807](https://doi.org/10.1127/njgpa/2019/0807).
- Ossó, À.**, 2021. Un cranc nou, *Eogeryon elegius* gen. nov., sp. nov. del Cenomanià tardà de la península Ibèrica. *Nemus* 11: 144–158.
- Ossó-Morales, À., Artal, P. & Vega, F.J.**, 2010. New crabs (Crustacea, Decapoda) from the Upper Cretaceous (Campanian) of the Moyenne Moulouya, northeast Morocco. *Revista Mexicana de Ciencias Geológicas* 27(2): 213–224.
- Phillips, GE, Nyborg, T, Vega, FJ**, 2013. Icriocarcinidae: a family of portunoid crabs from the Upper Cretaceous of North America. *Paläontologische Zeitschrift* 88(2): 139–158. DOI: [10.1007/s12542-013-0190-4](https://doi.org/10.1007/s12542-013-0190-4).
- Quayle, W.J. & Collins, J.S.H.**, 1981. New Eocene crabs from the Hampshire Basin. *Palaeontology* 24(4): 733–758, pls 104, 105.
- Rathbun, M.J.** Descriptions of fossil crabs from California. *Proceedings of the United States National Museum* 35(1647): 341–349, pls 45–49.
- Rathbun, M.J.**, 1932. Preliminary descriptions of new species of Japanese crabs. *Proceedings of the Biological Society of Washington* 45: 29–38.
- Rathbun, M.J.**, 1935. Fossil Crustacea of the Atlantic and Gulf Coastal plain. *In: Geological Society of America, Special Paper. 2, p. viii + 1-160.*
- Richards, B.C.**, 1975. *Longusorbis cuniculosus*: a new genus and species of Upper Cretaceous crab; with comments on Spray Formation at Shelter Point, Vancouver Island, British Columbia. *Canadian Journal of Earth Sciences* 12(11): 1850–1863.
- Saint Laurent, M. de**, 1980. Sur la classification et la phylogénie des Crustacés Décapodes Brachyours. I. Podotremata Guinot 1977 et Eubrachyura sect. nov. *Comptes Rendus de l'Académie des Sciences Paris*, D290, 1265–1268
- Saint Laurent, M. de**, 1989. La nouvelle superfamille des Retroplumoidea Gill, 1894 (Decapoda, Brachyura): systématique, affinités et évolution. *In: Forest J. (ed): Résultats des Campagnes MUSORSTOM, volume 5. Mémoires du Muséum national d'Histoire naturelle Paris, A. Zoologie. vol. 144, p. 103–179.*
- Schäfer, W.**, 1954. Form und Funktion der Brachyuren-Schere. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 489: 1–65.
- Schweitzer, C.E. & Feldmann, R.M.**, 2010. The Decapoda (Crustacea) as predators on Mollusca through geologic time. *Palaios* 25(3): 167–182.
- Schweitzer, C.E. & Feldmann, R.M.**, 2011. Revision of some fossil podotrematous Brachyura (Homolodromiidae; Longodromiidae; Tornyommidae). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 260(2): 237–256. DOI: [10.1127/0077-7749/2011/0138](https://doi.org/10.1127/0077-7749/2011/0138).
- Schweitzer, C.E. & Feldmann, R.M.**, 2012. Revision of Decapoda deposited in The Muséum national d'Histoire naturelle, Paris. *Bulletin of the Mizunami Fossil Museum* 38: 15–27.

- Schweitzer, C., Feldmann, R., Garassino, A., Karasawa, H., Schweigert, G.,** 2010. Systematic list of fossil decapod crustacean species. *Crustaceana Monographs* **10**: 1–222.
- Schweitzer, C.E., Feldmann, R.M., Karasawa, H.,** 2007. Revision of the Carcineretidae Beurlen, 1930 (Decapoda: Brachyura: Portunoidea) and remarks on the Portunidae Rafinesque, 1815. *Annals of Carnegie Museum* **76**(1): 15–37.
- Spiridonov, V.A.,** 2020. An update of phylogenetic reconstructions, classification and morphological characters of extant Portunoidea Rafinesque, 1815 (Decapoda, Brachyura, Heterotremata), with a discussion of their relevance to fossil material. *Geologija* **63**(1): 133–166. DOI: [10.5474/geologija.2020.014](https://doi.org/10.5474/geologija.2020.014).
- Štević, Z.,** 2005. The reclassification of brachyuran crabs (Crustacea: Decapoda: Brachyura). *Natura Croatica* **14**(Supplement): 1–159.
- Teodori, D., Ossó, Á., Nyborg, T. & Vega, F.,** 2013. The Icriocarcinidae (Brachyura, Portunoidea), a widely distributed family during the latest Cretaceous times. In: Krobicki M. (ed): 5th Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Abstract Book: 72. Polish Geological Institute, National Research Institute (Warszawa).
- Tesch, J.J.,** 1918. The Decapoda Brachyura of the Siboga-Expedition. I. Hymenosomidae, Retroplumidae, Ocypodidae, Grapsidae and Gecarcinidae. *Siboga Expeditie Monografie* **39**(c1): 149–295. DOI: [10.5962/bhl.title.10267](https://doi.org/10.5962/bhl.title.10267).
- Van Bakel, B.W.M., Jagt, J.W.M., Fraaije, R.H.B., & Coole, Y.,** 2003. New data on the crab *Binkhorstia ubaghsii* (Late Maastrichtian; NE Belgium, SE Netherlands). In: Jagt J.W.M., Van Bakel B.W.M. & Fraaije R.H.B. (eds): Second Symposium on Mesozoic and Cenozoic decapod crustaceans. Bostel/Maastricht, the Netherlands, September 3–6, 2003. *Contributions to Zoology*. **72**, 85–89.
- Van Bakel, B.W.M., Artal, P., Fraaije, R.H.B., & Jagt, J.W.M.,** 2010. *Loerenthopluma danielae*, a new crab (Decapoda, Brachyura, Retroplumidae) from the Lower Eocene of northwest Belgium, Studies on Brachyura: a homage to Danièle Guinot. In: Castro P., Davie P.J.F., Ng P.K.L. & Richer de Forges B. (eds): *Crustaceana Monographs*. vol. **11**, p. 41–49
- Van Bakel, B.W.M., Mychko, E.V., Spiridonov, A., Jagt, J.W.M., & Fraaije, R.H.B.,** 2023. New Cretaceous crabs (Crustacea, Brachyura) from Moscow Oblast and Dagestan (Russia): patterns in phylogeny and morphospace of the oldest eubranchyurans (Dorippoidea). *Cretaceous Research* **119**: 104675. DOI: [10.1016/j.cretres.2020.104675](https://doi.org/10.1016/j.cretres.2020.104675).
- Van Straelen, V.,** 1936. Crustacés décapodes nouveaux ou peu connus de l'époque crétacique. *Bulletin du Musée royal d'Histoire naturelle de Belgique* **12**(45): 1–50, pls 1–4
- Vega, F.J., Phillips, G.E. Nyborg, T., Flores-Ventura, J., Clements, D., Espinosa, B., & Solís-Pichardo, G.,** 2013. Morphology and size variation of a portunoid crab from the Maastrichtian of the Americas. *Journal of South American Earth Sciences* **47**: 116–135. DOI: [10.1016/j.jsames.2013.07.005](https://doi.org/10.1016/j.jsames.2013.07.005).
- Vía Boada, L.,** 1959. Decápodos fósiles del Eoceno español. *Boletín del Instituto Geológico y Minero de España* **70**: 331–402 [1–72], pls 1–7
- Withers, T.H.,** 1922. On a new brachyurous crustacean from the Upper Cretaceous of Jamaica. *Annals and Magazine of Natural History ser 9*. **10**: 534–541, pls. 16–17.
- Wolfe, J.M., Ballou, L., Luque, J., Watson-Zink, V.M., Ah Yong, S.T., Barido-Sottani, J., Chan, T.-Y., Chu, K.H., Crandall, K., Daniels, S.R., Felder, D.L., Mancke, H., Martin, J.W., Ng, P., Ortega-Hernández, K.L., Theil, J., Palacios, E., Pentcheff, N.D., Robles, R., Thoma, B.P., Tsang, L.M., R., Wetzer, Windsor, A.M., & Bracken-Grissom, H.D.,** 2023. Convergent adaptation of true crabs (Decapoda: Brachyura) to a gradient of terrestrial environments. *Systematic Biology* **73**(2): 247–262. DOI: [10.1093/sysbio/syad066](https://doi.org/10.1093/sysbio/syad066).
- Wright, C.W.,** 1997. New information on Cretaceous crabs. *Bulletin of the Natural History Museum London (Geology)* **53**(2): 135–138.
- Wright, C.W. & Collins, J.S.H.,** 1972. British Cretaceous crabs. Monograph of the Palaeontographical Society London **126**(533): 1–114, 22 pls