

Tribe Bembidiini

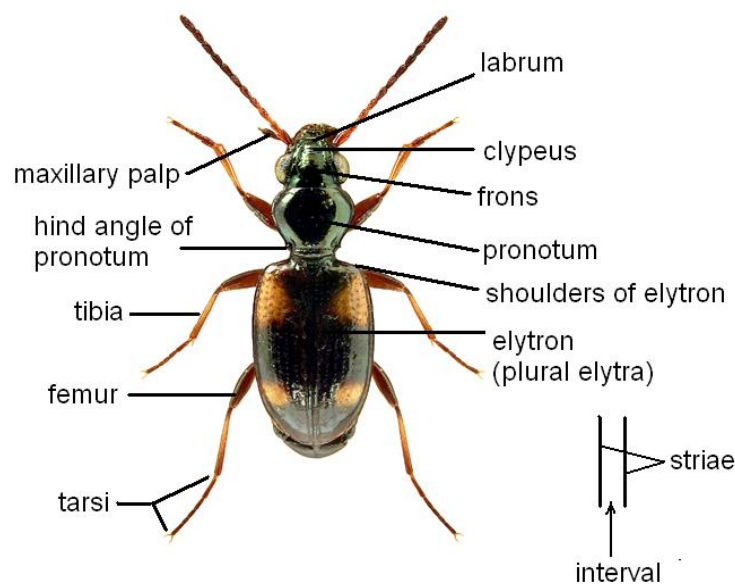
References

Translated and adapted for the British fauna by M Hackston

Müller-Motzfeld (2004) in Die Käfer Mitteleuropas, Band 2 Adephaga 1: Carabidae
Edited by Freude, Harde Lohse & Klausnitzer.

Müller (1918) Koleopterologische Rundschau Bd. 7 Bestimmungstabelle der
Bembidion-Arten Europas und des Mittelmeergebietes

A group of genera in which the last segment of the maxillary palps is rod-like and may be so small that it is hard to make out so the palps appear to be two-segmented with a club-shaped last segment.



Checklist of species

From the Checklist of Beetles of the British Isles, 2012 edition, edited by A. G. Duff.

Genus *Asaphidion* des Gozis, 1886

Genus *Bembidion* Latreille, 1802

Genus *Bracteon* Bedel, 1879

Genus *Cillenus* Leach, 1819

Genus *Elaphropus* Motschulsky, 1839

Genus *Ocys* Stephens, 1828

Genus *Tachys* Dejean, 1821

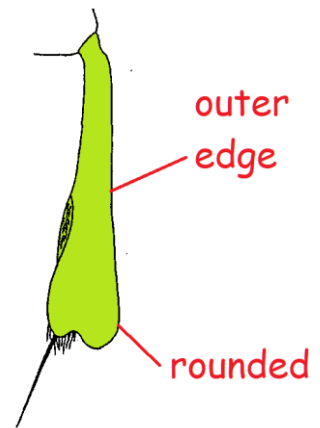
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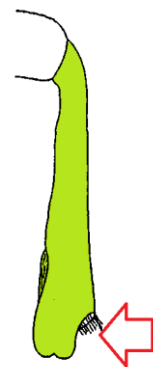


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1 Outer edge of the front tibiae straight, convex or rounded at the tip.2



Outer edge of the front tibiae straight to near the tip and then obliquely truncate or concave with a clear change of direction.6



- 2 Elytra randomly punctured with small patches of prostrate hairs; striae at most very weakly indicated. Head, measured across the eyes, at least as wide as the pronotum.
..... Genus *Asaphidion*



Elytra with distinctly indented striae, bare apart from isolated bristles. Head usually narrower than the pronotum.3



- 3 Head thickened with long, straight-projecting mandibles. Frons and pronotum lacking punctures. Elytra parallel-sided with complete, deep furrows; four bristle-bearing punctures present in the third stria. Upper surface dull with a coarse, net-like, isodiametric microscopic sculpture.

..... ***Cillenus lateralis***



(C) Udo Schmidt (2008)

Head not particularly thickened, distinctly narrowing behind the eyes. Only two bristle-bearing punctures on the third stria of the elytra or on the third interval. Mandibles shorter with the tips strongly inwardly curved.4



- 4 Sutural stria of the elytra running parallel to the suture to the tip and then curving round to follow the side of the elytra (similar to genus *Trechus*), there bordered by a clear fold. Upper surface more or less uniformly brown or with a metallic shine. Hind angle of the pronotum without a fold.
..... [Genus *Ocys*](#)

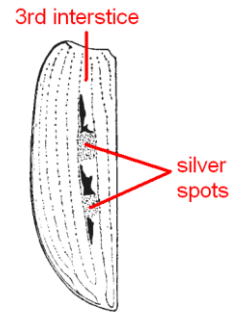


(C) Udo Schmidt (2008)

Sutural stria not curving round at the tip as above. Other features not in combination.5



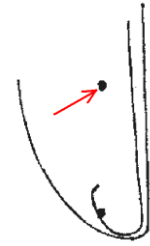
- 5 Third interstice of the elytra much broader than the second and fourth at middle and containing two distinct opaque patches (silvery spots).
..... Genus *Bracteon*



Third interstice of the elytra the same width as the adjacent ones.
..... Genus *Bembidion*



- 6 Posterior dorsal puncture of elytra situated well in front of the recurrent stria. Basal transverse impression of pronotum and at least the inner striae of the elytra with punctures. Convex species, strongly sclerotized (hardened). Upper surface shiny, microscopic sculpture absent or extremely fine (visible only at high magnification). Viewing the head from below, the labium lacks sharply defined impressions although sometimes with two grooves with indistinct edges or with longitudinal furrows ending in a small cavity.
 [Genus *Elaphropus*](#)



Posterior dorsal puncture enclosed within the hook of the recurrent stria. Pronotum with the basal impression smooth. Elytral striae shallow, without punctures or almost so. Flat species, with particularly the elytra weakly sclerotized. Upper surface dull, pronotum and elytra with dense transverse microscopic sculpture, more or less iridescent. Viewing the head from below the labium shows a pair of circular, deep, sharp-edged impressions.
 [Genus *Tachys*](#)



Genus *Asaphidion*

Distinguished from *Bembidion* mainly by the patchy hairs on the elytra and the bulging eyes. Pronotum heart-shaped, quite convex and very finely bordered at the sides. Elytra each with two large pore-punctures around the third interval. In males the first segment of the front tarsi is strongly dilated and the second is weakly so.

Genus **ASAPHIDION** des Gozis, 1886

curtum (Heyden, 1870) 5b

flavipes (Linnaeus, 1761) 5a

pallipes (Duftschmid, 1812) 8a

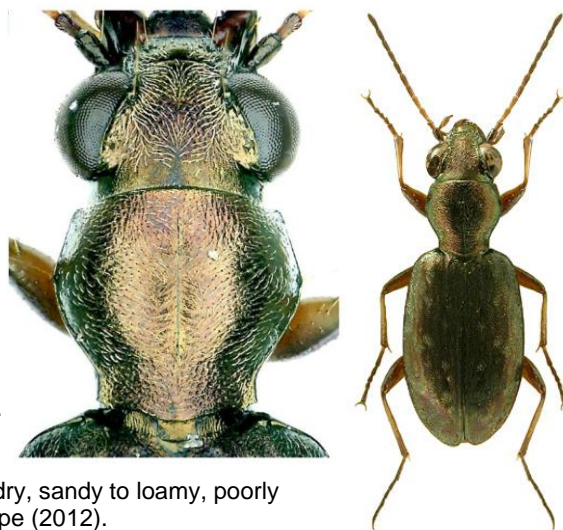
stierlini (Heyden, 1880) 35 4b

- 1 Hind angle of the pronotum next to the narrow lateral border with a short, straight furrow, which forms a sharp angle with the lateral border (sloping from the side when viewed from above); the hind angle bears a small bristle (often broken off). Punctures on the elytra larger, round and fairly dense.²
Take care. Until familiarity is gained with this character, the furrow is sometimes very difficult to see.

Hind angles of the pronotum without such a furrow - only the narrow lateral border is visible, which is slightly curved outwards. Elytra with the punctures finer, shallower and denser; elytra more wrinkled and leathery.

..... ***Asaphidion pallipes***

Basal segment of the antennae completely dark at least on the upper surface with a metallic shine (usually apparent on the second segment as well). Frons reddish with fine punctures in the distinct microscopic sculpture. Punctures on the elytra fairly clear. Coppery-reddish with grey-green spots. Europe except the Iberian Peninsula, Asia Minor and the Caucasus. In central Europe not uncommon, becoming rarer to the south west. On dry, sandy to loamy, poorly vegetated river banks. Close up diagram from Lompe (2012).



2¹ Elytra from the shoulders to the middle weakly, but distinctly rounded and therefore appearing more oval. Length 4.0-4.7 mm.3

Elytra distinctly parallel-sided. Length 3.0-4.2 mm. - the smallest British species. Ends of the tarsal segments and the last segments of the antennae clearly darkened and green-metallic. In the male, the first and second tarsal segments are only slightly broadened apically.

..... ***Asaphidion stierlini***

Southern England, northern France, Belgium, Holland and Austria (eastern Tyrol)



3² Apical half of the antennae and the knees distinctly darkened; knees with a more or less clearly defined green-metallic shine. Elytra coarsely punctured but with scarcely defined striae. Microscopic sculpture of the pronotum and elytra only weakly defined, the upper surface therefore appearing more shiny. Sides of the pronotum only slightly angled near the front lateral bristle. Greenish-brassy coloured. Length 4.0-4.7 mm.

..... ***Asaphidion flavipes***

Widespread in Europe except for the far north and the Iberian Peninsula. In open places but further south in cooler habitats at higher altitudes.



Antennae and legs not darkened or only slightly so. Punctures on the elytra somewhat finer and denser. Microscopic sculpture of the pronotum and elytra clearer so that the upper surface appears less shining; striae on the elytra clearer but still indistinct. Side margin of pronotum with a clearly angled near the front bristle. Background colour more reddish to coppery. Length 4.0-4.7 mm.

..... ***Asaphidion curtum***

European distribution uncertain due to historical difficulties with identification. Prefers more shady, wooded habitats. Photograph from Tree of Life website.



Genus *Bracteon*

Genus **BRACTEON** Bedel, 1879

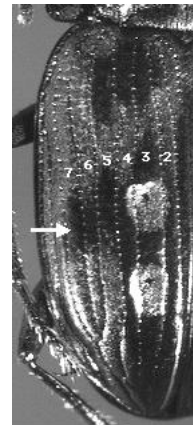
argenteolum (Ahrens, 1812)

litorale (Olivier, 1790)

- 1 Antennae completely black; legs dark brown; length 5-6 mm. Interstices 6 or 7 with mirrors as distinct or nearly as distinct as the mirrors in interstice 3, at or near the level of the silver spots.

..... ***Bracteon litorale***

Very local on sand gravelly banks of rivers in northern England and Scotland



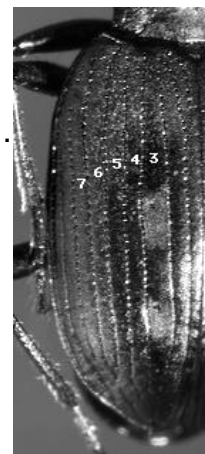
outer mirrors present



- Antennae black with segment one reddish at least underneath; tibiae red; length 5.5-7.0 mm. Interstices 6 or 7 lacking distinct mirrors, being more or less uniform in shine.

..... ***Bracteon argenteolum***

Northern Ireland



no outer mirrors



Genus *Ocys*

Genus **OCYS** Stephens, 1828

harpaloides (Audinet-Serville, 1821)

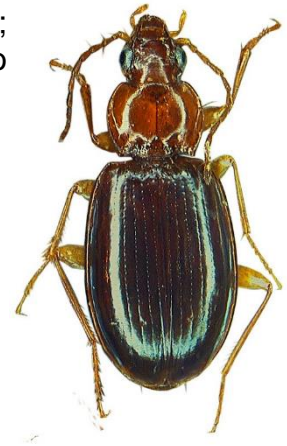
quinquestriatus (Gyllenhal, 1810)

Antennae and legs brownish yellow; head with two parallel frontal furrows; elytra with the striae petering out at the sides

- 1 Head and thorax reddish brown; elytra much darker in colour; larger species, 4.5-5.5 mm. Base of the pronotum straight so the hind angles are acutely angled. Elytra with only a single bristle-bearing puncture in the last third of the third stria.

..... ***Ocys harpaloides***

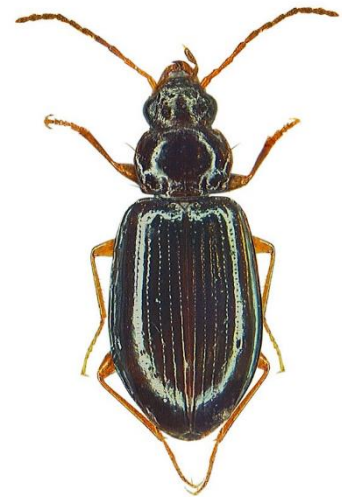
Local but widespread species found for example in damp moss and in damp logs in the winter



Head and pronotum black, with a slight bluish reflection not contrasting in colour with the elytra; smaller species, length 4.0-4.5 mm. Base of the pronotum more or less bevelled on each side so the hind angles are blunt and rounded. Elytra with two bristle-bearing punctures in the last third of the third stria.

..... ***Ocys quinquestriatus***

Local but widespread species found for example in damp moss



Genus *Elaphropus*

Genus **ELAPHROPUS** Motschulsky, 1839

parvulus (Dejean, 1831)

walkerianus (Sharp, 1913)

- 1 Smaller, more slender species, 1.7-2.4 mm. Elytra narrower and flatter, shining black. Antennae darkened from segment 3 or 4 onwards. Legs yellow brown. Fully winged. Elytra without microscopic sculpture near the scutellum. Elytral striae usually more distinctly punctured.

..... ***Elaphropus parvulus***

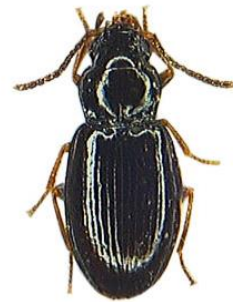
On open gravel often near the sea. England: Devon, Cornwall.



On average larger and broader, 2.0-2.5 mm. Sides of the elytra rather more rounded. Antennae darkened from the second segment; legs darker. Elytra with shallow, irregular microscopic sculpture (visible only at high magnification) between the reticulate scutellum and the basal pore-puncture. Elytra with 5 irregularly punctured striae.

..... ***Elaphropus walkerianus***

In *Sphagnum*. England: Hampshire and Surrey. Locally abundant.



Genus *Tachys*

Genus **TACHYS** Dejean, 1821

Subgenus **PARATACHYS** Casey, 1918

bistriatus (Duftschmid, 1812)

micros (Fischer von Waldheim, 1828)

obtusiusculus (Jeannel, 1941)

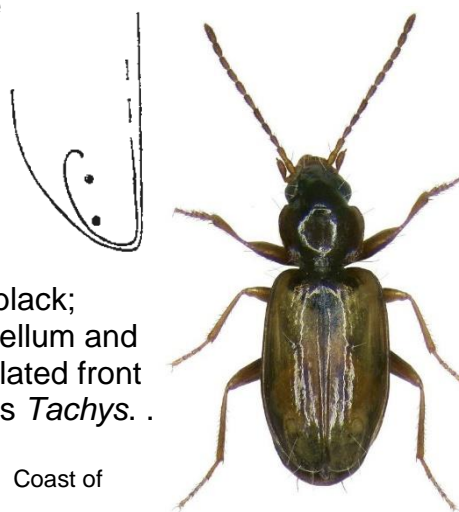
Subgenus **TACHYS** Dejean, 1821

scutellaris Stephens, 1828

- 1 Sutural stria of the elytra with strong hook at the end, extending well in front of the front dorsal puncture and passing this puncture some distance to the side. The four marginal punctures behind the shoulder of the elytra are almost equally distant from one another. Sides of pronotum not, or barely curving towards the base. Elytra blotched, striae somewhat more impressed. Head and pronotum dark brown to black; elytra brownish with a triangular spot about scutellum and usually also sides and apex dark. Male with 2 dilated front tarsal segments. Length 2.0-2.7 mm. Subgenus *Tachys*.

..... ***Tachys scutellaris***

In marshes and on mud, apparently dependent upon saline soil. Coast of southern and eastern England northwards to Norfolk.



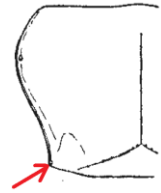
Sutural stria less hooked, ending a little beyond the front dorsal puncture and passing closely to this puncture. The distance between the third and fourth puncture behind the shoulders of the elytra is about twice the distance between the second and third. Sides of pronotum curving towards the rear. Elytra uniformly coloured or almost so. Male with only first front tarsal segment faintly dilated. Subgenus *Paratachys*[2](#)



2¹ Pronotum with the hind angles almost a right angle, the sides in front of them strongly curving, and base almost straight laterally. Reddish brown with only the head darker. Length 2.0-2.4 mm.

..... ***Tachys micros***

On patches of damp sand on coastal cliffs. England: Dorset, Sussex.



Pronotum with hind angles obtuse, rounded at tip; sides less curved, base oblique laterally. Body almost black to brown, head only slightly darker.³



3² Antennae more slender. Microscopic sculpture of pronotum and elytra fine and dense. First hind tarsal segment much longer than second and third combined. Wings normally developed. Length 1.8-2.3 mm.

..... ***Tachys bistratus***

On damp sand or clay at the border of standing and running fresh water, also on the coast. England northwards to Durham. South Wales.



Antennae, notably intermediate segments, much shorter. Microscopic sculpture coarser. First hind tarsal segment only slightly longer than second and third combined. Wings either normal or strongly reduced. Length 1.5-2.0 mm.

..... ***Tachys obtusiusculus***

In *Sphagnum*, associated with *Elaphropus walkerianus*. New Forest



Genus *Bembidion*

Checklist

From the Checklist of Beetles of the British Isles, 2012 edition, edited by A. G. Duff. Subgenus *Ocydromus* has been split into several subgenera by recent authors.

Genus *BEMBIDION* Latreille, 1802

Subgenus *Actedium* Motschulsky, 1864

pallidipenne (Illiger, 1802)

Subgenus *Bembidion* Latreille, 1802

humerale Sturm, 1825

quadrinaculatum (Linnaeus, 1761)

quadripustulatum Audinet-Serville, 1821

Subgenus *Bembidionetolitzkya* Strand 1929

atrocaeruleum (Stephens, 1828)

caeruleum Audinet-Serville, 1826

geniculatum Heer, 1837/8

tibiale (Duftschmid, 1812)

Subgenus *Diplocampa* Bedel, 1896

assimile Gyllenhal, 1810

clarkii (Dawson, 1849)

fumigatum (Duftschmid, 1812)

Subgenus *Emphanes* Motschulsky, 1850

minimum (Fabricius, 1792)

normannum Dejean, 1831

Subgenus *Neja* Motschulsky, 1864

nigricorne Gyllenhal, 1827

Subgenus *Metallina* Motschulsky 1850

lampros (Herbst, 1784)

properans (Stephens, 1828)

Subgenus *Princidium* Motschulsky, 1864

punctulatum Drapiez, 1821

Subgenus *Eupetedromus* Netolitzky, 1911

dentellum (Thunberg, 1787)

Subgenus *Lymnaeum* Stephens, 1828

nigropiceum (Marsham, 1802)

Subgenus *Nepha* Motschulsky, 1864

illigeri Netolitzky, 1914

Subgenus *Notaphus* Dejean, 1821

obliquum Sturm, 1825

semipunctatum (Donovan, 1806)

varium (Olivier, 1795)

Subgenus *Notaphemphanes* Netolitzky, 1920

ephippium (Marsham, 1802)

Subgenus *Ocydromus*

bruxellense Wesmael, 1835

bualei Jacquelin du Val, 1852

decorum (Zenker in Panzer, 1800)

deletum Audinet-Serville, 1821

femoratum Sturm, 1825

fluviatile Dejean, 1831

lunatum (Duftschmid, 1812)

maritimum (Stephens, 1835)

monticola Sturm, 1825

saxatile Gyllenhal, 1827

stephensii Crotch, 1866

testaceum (Duftschmid, 1812)

tetracolum Say, 1825

Subgenus *Philochthus* Stephens 1828

aeneum Germar, 1824

biguttatum (Fabricius, 1779)

guttula (Fabricius, 1792)

iricolor Bedel, 1879

lunulatum (Duftschmid, 1812)

mannerheimii Sahlberg, C.R., 1827

Subgenus *Phyla* Motschulsky, 1844

obtusum Audinet-Serville, 1821

Subgenus *Plataphus* Motschulsky, 1864

prasinum (Duftschmid, 1812)

Subgenus *Pseudolimnaeum* Kraatz, 1888

inustum Jacquelin du Val, 1857

Subgenus *Semicampa* Netolitzky, 1910

gilvipes Sturm, 1825

schuppelii Dejean, 1831

Subgenus *Sinechostictus* Motschulsky, 1864

stomoides Dejean, 1831

Subgenus *Testedium* Motschulsky 1864

bipunctatum (Linnaeus, 1761)

Subgenus *Trepanedoris* Netolitzky, 1918

doris (Panzer, 1796)

Subgenus *Trepanes* Motschulsky, 1864

articulatum (Panzer, 1795)

octomaculatum (Goeze, 1777)

Subgenus *Trichoplataphus* Netolitzky, 1914

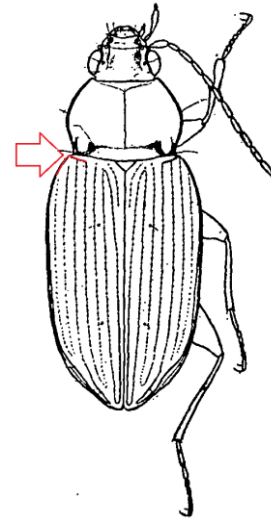
virens Gyllenhal, 1827



Key to subgenera and species

Translated from Müller (1918) Koleopterologische Rundschau Bd. 7
Bestimmungstabelle der Bembidion-Arten Europas und des Mittelmeergebietes

- 1 The outer part of the basal margin of the elytra is more or less clearly raised, forming an angle with the side margin.2



Basal margin of the elytra completely absent or short and forming a curve into the side margin.5



- 2 Eighth stria of the elytra similar to the rest of the stria, clearly punctured and separated from the ninth stria which is close to the margin by a broad interval. [Genus *Bracteon*](#)

Eighth stria much more incised than the ones closer to the suture, usually smooth and only narrowly separated from the margin.3



- 3 Upper surface with a metallic shine. Elytra either with a fine reticulate surface sculpture or smooth.4

Upper surface brown or black. Elytra with an extremely fine and dense microscopic sculpture of transverse ridges. **Subgenus *Phyla***
..... ***Bembidium obtusum***
Common and widespread on heavy soils



- 4 Ridge on the frons doubled with a longitudinal furrow in between; the front supraorbital puncture is located on the front end of the ridge. **Subgenus *Neja***
 ***Bembidion nigricorne***
 A widespread but very local and scarce heathland species.



- Ridge on the frons single.
 **Subgenus *Metallina***

Pronotum strongly heart-shaped, clearly tapering towards the base with large right-angled hind angles. Striae of the elytra fading towards the tip, becoming indistinct or absent, leaving the preapical puncture isolated, not in a stria. Upper surface shining and smooth. Elytra usually bronzy without paler patches, rarely bluish or black



- 5 Sutural stria continuing around the tip of the elytra or not; if continuing then it is not bordered by a ridge.6

Sutural stria continuing around the tip of the elytra and here bordered by a clear ridge. Usually reddish brown or dark brown species with a broad pronotum and parallel frontal furrows. Elytra usually without a dorsal puncture in front part of the basal half.

..... [Genus *Ocys*](#)



- 6 Frontal furrows shallow or indistinct, difficult to make out amongst the punctures on the frons that run together into parallel ridges.7

Head usually smooth (rarely partly punctured) so that the frontal furrows are always clear and incised with a smooth fold in between.9



- 7 All striae on the elytra sharply incised right the way to the tip. **Subgenus *Principidium***
 ***Bembidion punctulatum***
 A generally rare species in the south east in wetland marginal habitats



Striae becoming much finer and less incised or fading completely towards the tip and usually also towards the sides.8



- 8 The entire upper surface is dark metallic with at most the tip of the elytra reddish yellow. Seventh striae of the elytra sharply incised towards the tip with the preapical bristle-bearing puncture within it. Both dorsal punctures of the elytra large and deep. **Subgenus *Testedium***.
 ***Bembidion bipunctatum***
 A widespread but very local and generally rare wetland species



Elytra brownish yellow with darker markings. Seventh striae of the elytra completely faded towards the rear so the preapical bristle-bearing puncture is isolated and not in a stria. Both dorsal punctures of the elytra are small. **Subgenus *Actedium***.
 ***Bembidion pallidipenne***
 A widespread but generally scarce maritime species



- 9 Sides of the pronotum rounded right up to the blunt hind-angles; base of the pronotum more or less strongly concave each side. Furrows on the frons parallel. Elytra with the sutural stria curving around at the tip and with the marginal ridge curving round at the base of the shoulders and visible from above (clavicular ridge).
..... **Subgenus *Philochthus***

Sides of the pronotum concave before the hind angles.10



10 Frontal furrows usually parallel and not extending onto the clypeus between the bristles at the front edge.11

Frontal furrows extended onto the clypeus and converging at least at the front – the extension runs between the bristles on the clypeus.22



11 The dorsal bristle-bearing punctures on the elytra are located on the third stria.
.....12

The dorsal bristle-bearing punctures on the elytra are located in the third interval
.....19



- 12 Eighth striae of the elytra shortened at the front or merging with the marginal stria already in the rear third. Process of the metasternum between the middle coxae not bordered. Elytra with coarse striae which usually fade towards the tip often leaving the preapical puncture isolated. **Subgenus *Sinechostictus***
 ***Bembidion stomoides***



Eighth striae of the elytra not as shortened and merging with the marginal stria in the front third.13



- 13 Middle line of the pronotum broadening in the basal third forming a furrow sharply bordered each side (rarely simple but then the sides of the mesothorax are punctured). Brown or black, with at most a slight metallic shine, with small flat eyes. Process of the metasternum not bordered. **Subgenus**
Pseudolimnaeum.
 *Bembidion inustum*

Middle line of the pronotum finely incised towards the base or fading.
 Mesothorax always without punctures.14



- 14 The rear supraorbital bristle is fine and is further from the eye margin and inserted distinctly behind the eye. Elongate species with the head and pronotum almost equal in width and slightly narrower than the elytra. Elytra flattened with complete striae. Upper surface brown or black with a metallic shine. Process of the metasternum bordered. **Subgenus *Limnaeum***.
..... ***Bembidion nigropiceum***



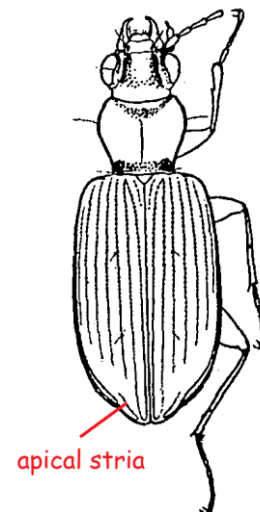
The rear supraorbital bristle is inserted on the imaginary line between the hind margin of the eyes. Body broader. Head and pronotum considerably narrower than the elytra. At least the head and pronotum are clearly metallic.15

15 Process of the metasternum between the middle coxae not bordered towards the tip. Usually uniformly dark green with the striae of the elytra incised right to the tip. Upper surface with a reticulate microscopic sculpture. Legs and antennae dark with at most the first segment of the antennae reddish.16

Process of the metasternum bordered right to the tip. Seventh striae of the elytra commonly shortened or erased.18



- 16 On the elytra at least the inner striae extend beyond clearly beyond half way. An apical stria is present near the margin of the elytra near the tip. Pronotum usually broader and flatter.17



Striae of the elytra only really clear in the basal half, becoming indistinct or erased leaving the preapical puncture isolated. Apical stria indistinct or absent. Pronotum narrow, domed and strongly heart-shaped. **Subgenus *Nepha***
..... ***Bembidion genei*** subspecies ***illigeri***
A locally common species of wetland margins in southern and eastern England



17 Elytra with the second striae evenly incised to the tip. Parameres with three bristles. Base of the pronotum usually smooth (sometimes weakly punctured in *B. coeruleum*) with a distinct angular fold. Elytra with a microscopic reticulate sculpture all over; pronotum with such sculpture at least near the base and towards the sides. Upper surface either uniformly metallic blue or green, sometimes with the elytra two-coloured. In species with completely or partly metallic elytra, usually only the first segment of the antennae is reddish.
..... **Subgenus *Bembidionetolitzky***

Elytra with the second striae becoming finer or fading completely (rarely continuing incised to the tip but then lacking the combination of features above). Parameres with four bristles (except *B. monticola*, which has pale legs).
..... **Subgenus *Ocydromus***



- 18 Abdominal sternites with the two normal bristle-bearing punctures. First segment of the antennae usually reddish below. **Subgenus *Plataphus***
..... ***Bembidion prasinum***

A very local species of wetland margins across Wales, northern England and Scotland



- Abdominal sternites with a row of bristle-bearing pores just before the rear edge. Striae on the elytra incised to the tip but the inner ones are clearer while the outer striae are finer. **Subgenus *Trichoplataphus***
..... ***Bembidion virens***

A very local species of sandy and gravelly waterside habitats in the north of Scotland



19 Elytra with the striae incised all the way to the tip.20

Elytra fading towards the tip so that the preapical puncture is isolated. Pronotum shining, distinctly heart-shaped and convex with small elongate basal impressions.

..... [Subgenus *Emphanes*](#)



- 20 At least the head and pronotum with a clear reticulate surface sculpture. Elytra brownish yellow with darker zig-zag markings and patches or greenish black (rarely blue-black) with yellow markings. Antennae dark for the most part.21

Upper surface almost completely smooth without a reticulate surface sculpture. Antennae, legs and elytra pale yellow. Elytra usually with a dark patch behind the middle which joins across the suture. Antennal furrow complete and sharp. Length 2.5-3 mm. **Subgenus *Notaphemphanes***.

..... ***Bembidion ephippium***

A very local south-eastern maritime species



- 21 Length 5-6 mm. Frontal furrows sharply indented behind the front supraorbital puncture, the area around raised and more shining than the frons. Elytra with a microscopic sculpture of transverse wrinkles. **Subgenus *Eupetedromus***.
 ***Bembidion dentellum***
 Widespread and very common.



Length 3-5 mm. Frontal furrows around the front supraorbital puncture flattened and soon after becoming indistinct; the area around is not raised into wrinkles. Elytra with a transverse reticulate microscopic sculpture.
 **Subgenus *Notaphus***



22 Furrows on the frons between the eyes more or less parallel and then clearly converging on the clypeus. Clavicular ridge absent or rudimentary. Pronotum usually flatter. Elytra more rounded at the sides. Upper surface often with a microscopic reticulate surface sculpture.23

Furrows on the frons either converging strongly throughout their length or if parallel between the eyes and then converging, then the clavicular ridge is completely developed (a continuation of the marginal ridge at the base of the elytra around the shoulder towards the centre line). Body usually narrower and more elongate. Pronotum strongly heart-shaped and convex. Upper surface always distinctly shining without a microscopic sculpture.24



23 Frontal ridge between the furrows doubled only near the front.
..... **Subgenus *Semicampa***

Frontal ridge between the furrows doubled along its whole length.
..... **Subgenus *Diplocampa***



24 The small tooth-like hind angles of the pronotum are shifted forwards by a short, angular incision at the base of the pronotum. Just above the basal margin there is a continuous transverse furrow so that there are no further impressions next to the middle. Frontal furrows weakly converging.
..... **Subgenus *Bembidion***

Hind angles of the pronotum not clearly removed forwards. Central part of the pronotum near the base with or without additional impressions. If there is a continuous transverse furrow close to the base of the pronotum then the frontal furrows are straight and strongly converging.25



25 Process of the metasternum unbordered between the middle coxae. Clavicular ridge absent. Tip of the aedeagus broadened like an anchor. **Subgenus *Trepanedoris***

..... ***Bembidion doris***

A generally common species across the southeast but otherwise less frequent elsewhere except for the far north, it occurs in a range of wetland habitats.



Process of the metasternum bordered between the middle coxae. Clavicular ridge present.

..... **Subgenus *Trepanes***



Subgenus *Bembidion*

- 1 Elytra with four yellow patches.2

Elytra each with a single small marking over the shoulder.
Antennae, palps and femora black. Tibiae reddish
yellow. Length 2.5 mm.

..... *Bembidion humerale*



- 2 Antennae black, at most segments 3-4 with a reddish base. Length 3-4 mm.
..... ***Bembidion quadriguttatum***

Antennae with the first four segments reddish yellow for the most part. Length 2.5-3.5 mm.
..... ***Bembidion quadrimaculatum***
Widespread and generally common



Subgenus *Bembidionetolitzkya*

- 1 Base of the pronotum clearly oblique on either side next to the hind angles. Hind angles weakly obtusely angled to right-angled. Pronotum usually smaller and narrower towards the base.2

Base of the pronotum at most scarcely oblique, sometimes slightly concave next to the hind angles. Hind angles usually clearer, right-angled to acutely angled.



- 2 Elytra rather pointed at the tip. Any microscopic sculpture in the middle of the pronotum is usually indistinct or absent (base clearly punctured). Length 6-7 mm.
..... ***Bembidion caeruleum***



- Elytra more broadly rounded at the tip. Pronotum with a clear reticulate surface sculpture over the whole surface. Length 4-5 mm.
..... ***Bembidion atrocaeruleum***



- 3 Elytra with a microscopic sculpture of narrow reticulations, much broader than long; elytra rounded at the tip. Length 4.5-6 mm.
..... ***Bembidion tibiale***
Widespread, but more common in the north



- Elytra with the surface reticulation almost isodiametric or weakly transverse.
..... ***Bembidion geniculatum***



Subgenus *Diplocampa*

- 1 Pronotum with a general leathery surface sculpture and therefore appearing duller in the middle than the elytra.2

Pronotum with a weaker reticulate surface sculpture, as shining in the middle as the elytra are. Elytra black with a greenish sheen with at most a weak preapical paler marking, although sometimes with the tip brownish or translucent reddish. Length 3-3.3 mm. ...

..... ***Bembidion clarkii***

Widespread and may be locally common



- 2 Smaller more convex species with shorter antennae. Striae of the elytra deeply incised. Black with a slight greenish sheen with a preapical paler marking (rarely absent) and with the tip itself more or less brownish-yellow. Length 2.8-3 mm.

..... ***Bembidion assimile***

Widespread and may be locally common



Larger, flatter species with more elongate antennae and finer striae on the elytra. Elytra always with numerous elongate pale patches in the basal half along with a vague zig-zag transverse band in the rear third and a brownish yellow tip. Length 3.5-3.8 mm.

..... ***Bembidion fumigatum***

Generally scarce and mostly coastal.



Subgenus *Emphanes*

- 1 Clavicular ridge complete. Upper surface metallic black; palps, antennae and legs black or dark brown; sometimes the tips of the elytra are paler brown. Length 2.5-2.8 mm.
..... ***Bembidion minimum***



Clavicular ridge shortened. Pronotum narrower and elytra more convex in section with less obvious, more broadly-rounded shoulders and coarser striae on the elytra. Upper surface dark metallic green. Elytra reddish in the apical part. Antennae brown with the basal segment reddish yellow. Pronotum with a row of unequal, large punctures immediately before the narrowly waisted basal margin. Length 2.5-3.2 mm.
..... ***Bembidion normannum***



Subgenus *Metallina*

- 1 Elytra with six coarse striae. On average smaller.
..... ***Bembidion lampros***
Generally abundant in dry habitats



Elytra with the 7th striae distinct at least towards the front; striae relatively less incised. On average larger.
..... ***Bembidion properans***
Widespread species



Subgenus *Notaphus*

- 1 Elytra with the tip and the epipleura brownish yellow. Legs brownish yellow at most in part with a greenish sheen.2

Elytra with the epipleura and the tips usually dark. Legs normally blackish. Elytra with the striae relatively more finely incised. Upper surface dark bronzy-green or blackish; elytra with two, narrow, yellowish zig-zag bands (rarely also with a yellow tip). Length 3.5 mm

..... ***Bembidion obliquum***

Widespread and may be locally common, in damp habitats



- 2 Larger, darker species with more elongate and usually more finely striated elytra. Pronotum strongly narrowing towards the rear. Shoulders of the elytra distinctly rounded, interrupting the outline of the elytra. Antennae with segments 3-4 only reddish on the underside. Elytra with more extensive black colouring over the shoulders extending right up to the edge (viewed from above). Length 4-5 mm.

..... ***Bembidion varium***

Widespread and may be locally common, in damp habitats



Smaller, paler species with shorter elytra with more incised striae. Pronotum less narrowing to the rear, usually broader towards the base than across the front margin. Outline of the elytra around the shoulders evenly curved. Antennae with segments 3-4 reddish yellow for the most part. Elytra brownish yellow around the shoulders or at most with a small dark oblique marking which does not reach the edge, viewed from above.

..... ***Bembidion semipunctatum***

Generally rare species in the south east, in damp habitats



Subgenus *Ocydromus*

- 1 Rear part of the head adjacent to the frontal furrows more or less distinctly punctured. The whole elytra have a very fine and dense transversely-wrinkled microscopic texture.2

Rear part of the head smooth, rarely with a few punctures but then the elytra is not textured as above.3



- 2 Elytra uniformly blue or blue-green, rarely brownish. Second to last segment of the palps usually blackish. Length 5.5-6 mm.
..... ***Bembidion decorum***



Upper surface greenish or metallic. Elytra with a large paler patch with vague edges extending from the shoulders and a sharply-defined preapical patch. In a form from the Isle of Wight (*vectense*) the elytra are brownish yellow with a paler preapical marking and a greenish tip. Length 4-5 mm.
..... ***Bembidion saxatile***



- 3 Pronotum without a postangular ridge. Elytra brownish-yellow with a weak greenish sheen and with indistinct paler patches. Segments 1-3 of the antennae and the legs completely pale. Length 4.5-5.5 mm.
..... ***Bembidion testaceum***



Pronotum with a postangular ridge.4



- 4 Elytra uniformly metallic, at most translucent reddish at the tip or uniformly brownish yellow with a more or less distinct metallic shine – never clearly spotted or banded paler.5



Elytra dark, metallic, clearly yellowish or reddish in the apical third or near the tip.

..... ***Bembidion lunatum***

Very local species of riversides. Now placed in subgenus *Asioperyphus*



Elytra either dark metallic with paler patches over the shoulders and before the tip OR with extensive paler markings with a dark cross-shaped pattern separating them into four.8



- 6 Pronotum with a distinct reticulate surface texture over the whole surface. Elytra with a microscopic texture of extremely fine and dense transverse wrinkles. Upper surface blue. Antennae blackish with the basal segments reddish yellow. Legs uniformly reddish yellow. Length 4.5-5 mm.

..... ***Bembidion monticola***

A rare and local species occurring sporadically in the south of England and Wales and in Scotland. Now placed in subgenus *Peryphiolus*



Pronotum smooth at least in the middle.7



- 7 Elytra with a distinct reticulate surface texture towards the base. Upper surface greenish. Elytra at most translucent reddish towards the tip. Length 5-6.3 mm.
 ***Bembidion stephensii***
 A generally rare wetland species. Now placed in subgenus *Peryphanes*



- Elytra with a weak reticulate surface texture restricted to the tip. Upper surface metallic blue or green. Length 5-6 mm.
 ***Bembidion deletum***
 Locally common in a variety of habitats. Now placed in subgenus *Peryphanes*



- 8 Surface of the pronotum completely covered with a distinct transversely-reticulate surface sculpture. Length 4.5-5 mm.

..... ***Bembidion bruxellense***

Widespread and common in wetland habitats. Now placed in subgenus *Peryphus*.



- Surface of the pronotum at least in the middle smooth when viewed with a microscope.9



- 9 Pronotum usually distinctly broader than long with the normal lateral keel and clearly marked front angles.10

Pronotum strongly convex in section, at most scarcely broader than long with the front angles truncate or weakly rounded. Elytra with the 7th striae marked by a row of quite strong punctures. Antennae black from the 4th or 5th segment onwards. Length 5.5-6 mm.
..... ***Bembidion fluviatile***



- 10 Elytra with the darker transverse band shortened at the sides so that the paler shoulder patches and preapical patches are united along the margin; patches over the shoulders broadly divided across the suture by black from the 3rd or 2nd striae. Antennae, palps and legs uniformly reddish-yellow. Elytra with a microscopic texture of broad reticulations; 7th striae completely absent. Length 5-5.5 mm.
..... ***Bembidion maritimum***



Elytra with the darker transverse band running right across from one side to the other so the front and rear paler patches are completely separate.11



- 11 Elytra with the 7th striae clearly visible in the front half. Tips of the elytra dark metallic. Elytra each with a reddish brown shoulder patch and a slightly paler preapical mark. Length 5-6 mm.

..... ***Bembidion tetracolum***

Very common and widespread. Now placed in subgenus *Peryphus*.



Elytra with the 7th striae completely erased.12



- 12 Antennae with at most the two basal segments completely yellowish red. Maxillary palps black for the most part. Femora usually darkened. Elytra with the black cross-shaped marking with a weak metallic shine. Pronotum and elytra proportionally narrower with the shoulders less projecting. Length 4.5-5 mm.
..... ***Bembidion femoratum***



- Antennae with at least three reddish yellow segments at the base. Maxillary palps with at most the second to last segment is darkened. Cross-shaped black marking on the elytra distinctively metallic blue or green. Length 4.5-5.2 mm.
..... ***Bembidion bualei***



Subgenus *Philochthus*

- 1 Elytra with the 7th stria present. Length 3.5-4 mm.
..... ***Bembidion biguttatum***



Elytra with the 7th stria absent.2



2 Pronotum with a microscopic reticulate sculpture towards the front and rear margins; central part with a smooth mirror-like shine.3

Pronotum with a microscopic reticulate sculpture all over the surface.4



- 3 Larger species, 4.5-5.5 mm. Antennae very slender. Slightly iridescent. Elytra with less deeply incised striae.
..... ***Bembidion iricolor***



Smaller species, 3-4 mm. Antennae rather shorter. Elytra with the striae on the front half more deeply incised. Black with a weak iridescence. Tips of the elytra brownish yellow along with a lateral marking behind the middle – these may be joined along the margin.
..... ***Bembidion lunulatum***
A coastal species.



- 4 Larger and flatter species with a greenish or bronzy shine. Head always with a distinct leathery surface texture and thus dull. Pronotum appearing dull even using a hand lens. Elytra bronzy or brownish metallic shining with paler edges. Antennae generally more slender. Elytra usually with finer striae. Length 3-4.2 mm.
 ***Bembidion aeneum***



Smaller, more convex species, black or brown. Head less dull. Pronotum shining, at least in the middle. Elytra pitchy black or brown, without a metallic sheen, at most weakly greenish or bluish iridescent. Striae on the elytra usually more incised. Antennae more compact. Length 2.8-3.3 mm.5



- 5 Pronotum broader in proportion to the elytra, often almost as wide; elytra tending to be shorter and more convex - the combined width divided by the length, between 0.63-0.74. Upper surface pitchy black or brown without a metallic shine. If an elytron is splayed from the body, the apical part shows at most a very faint paler area and the wings are reduced to a tiny vestige. Length 2.8-3 mm.
 ***Bembidion mannerheimii***



Pronotum slimmer, comparatively narrower compared with the elytra. Elytra appearing narrower, more elongate, flatter and less rounded at the sides - the combined width divided by the length, between 0.6-0.7. Pitchy black or brown with a weak, sometimes bluish sheen (only apparent in fresh specimens). Elytra with a paler patch before the tip, but this requires the elytra to be opened a bit to see clearly. If the elytra are splayed the wings underneath are usually fully-developed, extending at least ¾ of the length of the elytra or in a minority of specimens they are greatly reduced, narrow and only reaching at most ½ the length of the elytra. Length 2.8-3 mm.
 ***Bembidion guttula***



Subgenus *Semicampa*

- 1 Elytra with a transversely reticulate surface sculpture all over. Femora black for the most part. Length 2.5-3 mm.
..... ***Bembidion schuppelii***
Northern England and southern Scotland

Elytra smooth with a surface sculpture only near the extreme tip. Upper surface shining, black. Antennae black with the first two segments reddish yellow. Length 2.5-2.8 mm.
..... ***Bembidion gilvipes***
Widespread but more common in the north of England



Subgenus *Trepanes*

- 1 Pronotum appearing narrowly heart-shaped, usually clearly narrower towards the base than the width of the head measured behind the eyes. Basal part of the elytra reddish yellow or black, without yellow elongate markings.

..... ***Bembidion articulatum***

One of the most common species of wetland margins.



Pronotum much broader than long, at least as wide near the base as the head behind the eyes. Elytra black with a preapical marking in the rear third and several elongate yellow markings in the front half.

..... ***Bembidion octomaculatum***

A very rare species of the south and southeast; it was for a long time considered extinct in the UK but since its rediscovery in the early 1990's seems to be spreading.



Variations in morphology within genus *Bembidion*

Frontal furrows

On the head, the frontal furrows provide important systematic characteristics. It is hypothesised that the simple parallel-sided furrows are the original character because it is combined with the partially raised basal border of the elytra and the striae of the elytra continuing incised to the tip. Derived characters of the frontal furrows are the extensions of the furrows onto the clypeus and a doubling of the furrows.

The development of the frontal furrows onto the clypeus can be seen in subgenus *Emphanes*. *B. normannum*, *lais*, *latiplaga* and *minimum* show the original type. In *B. moeoticum* two fine oblique lines are present on the clypeus, a continuation in the line of the deep, parallel frontal furrows, which begin to converge towards the front. In *B. 4-plagiatum* and *tenellum* the furrows start to converge well basal to the clypeus and continue strongly onto the clypeus itself. The strongest convergence is found in the closely related subgenus *Trepanes* where the deep and almost completely straight furrows meet on the front edge of the clypeus.

The doubling of the frontal furrows occurs in the area between the furrows and the inner margin of the eyes and sides of the clypeus. This area may be termed the frontal fold (Stirnfall) and within this area are found the two bristle-bearing supraorbital punctures. In the simplest case the frontal folds are evenly curved or flat; in derived forms there may be a fine longitudinal furrow which gives the appearance of a double furrow. This is present in the rear part of the frons in subgenus *Neja*, the front part, extending onto the clypeus in subgenus *Semicampa* and along the entire length in subgenus *Diplocampa* where it is described as a double frontal furrow.

The doubling of the furrows does not correlate with the elongation of the frontal furrows onto the clypeus. There are forms such as subgenera *Trepanes* and *Noaphocampa* which have strongly convergent furrows that extend to the front margin of the clypeus and simple, broad frontal furrows.

The eyes, temples and the posterior supraorbital puncture

The size and curvature of the eyes is also important along with their length relative to the temples. It is hypothesised that the plesiomorphic state is large and more bulging eyes and short temples which are more sharply differentiated from the neck. There is a tendency for derived forms to have flatter eyes and longer temples which grade into the neck. This is correlated to the position of the posterior supraorbital puncture which in large-eyed forms is close to the inner margin of the eye and before an imaginary line joining the hind margins; in small-eyed forms (e.g. subgenera *Limnaeum* and *Oreocys*) they are further from the eyes and are behind the line joining the hind margins. These differences are not due to a shift in the location of the supraorbital puncture but to a shortening of the diameter of the eye.

Pronotum



The hypothesised plesiomorphic state is found in subgenus *Pogonidium* which bears a close resemblance to genus *Pogonus*. Here the pronotum is broad and flat, broadest at about half way and tapering from there more strongly towards the front than to the rear. The front angles are somewhat projecting and the sides are weakly concave before the hind angles. The hind angles are sharply right-angled. The base is broad, flat and straight; in front of the base are two basal impressions each side (often seen in Carabidae), of which the inner one is distinctly hollowed and the outer is more linear, indicated only by a raised outer ridge. The inner impressions are termed basal impressions (*Basalgruben*) and the outer ones the postangular ridges (*Postangularfältchen*). Between the hind angles and the basal impression the base is finely bordered; then this fine border bends forwards forming a short linear furrow at the base of the basal impressions. The basal surface within the impression is not bordered and forms a broad bulge, with a weak transverse depression in front. The sides are narrowly bordered and the low keel on the side bears the anterior marginal bristle in the middle. The posterior marginal bristle arises from the hind angle itself. The middle line is fine and slightly impressed.

Any variations from this type can be regarded as derived characters. The most common is a narrowing of the basal part, leading to a heart-shaped appearance. In addition the dorsal surface may become convex in section. The border along the side may be finer, the front angles obtuse and the basal impressions appear to be much closer to the sides due to the constricted basal part. The postangular ridges may appear to be merged with the outer edge of the basal impressions rather than there being a gap between them.

This is developed to an extreme in subgenus *Metallina* (*lampros*, *pygmaeum*) but intermediates are found in subgenera *Neja* and *Chlorodium*. Similar changes in the form of the pronotum are seen in other groups, for example in *Bembidionetolitzkya* and *Ocydromus* through to the greatest development in subgenus *Nepha* where the development is even more developed than in *Metallina*. Here the narrowing and the curvature of the pronotum is so strong that the basal part closely surrounds the mesosternal stalk (in *Metallina* it is still significantly broader than the stalk). In *Bembidion* the tiny tooth-like hind angles appear to be shifted forwards due to a tiny incised section at the base.

Another direction of development is seen in subgenus *Philochthus*. Here there is a general reduction in the hind angles and the adjacent basal part of the pronotum. The hind angles are obtuse and the border disappears; at the same time the width of the base shrinks between the mesosternal stalk and the hind angles so that the basal border has a rather extensive transverse groove alongside it. The rear angles appear to be slightly shifted forwards but they are still well-marked (e.g. *B. guttula* and *B. biguttatum*). If there is a narrowing of the whole base of the pronotum, the hind angles are almost completely rounded and the basal groove is no longer transverse but diagonal towards the mesosternal stalk (e.g. *B. inoptatum* and *decolour*). There is an indication of the condition found in *Philochthus* in genus *Ocys*. Here the base of the pronotum is slightly oblique from the hind angles; also the sides are at most scarcely concave in front of the hind angles.

Other features of the pronotum are regarded as derived characters:

- The absence of the postangular ridges (e.g. in *B. testaceum*),



- The presence of punctures in front of the base of the pronotum (e.g. some species of subgenus *Ocydromus* and *Sinechostictus*)
- The formation of a basal swelling with a sharply linear border (*Bembidion*, *Trepanes*)
- Further depressions within the normal basal impressions
- Absence of the anterior marginal seta (some species of subgenus *Chrysobracteon* – *B. argenteolum* and *B. litorale*)

Elytra

a) Striae

The elytra offer the greatest variety of characters both in general shape and sculpture. The hypothesised plesiomorphic state is having the elytra quite elongate with more or less parallel sides and well-marked shoulders. The secondary flattening of the shoulders increases the curvature of the sides of the elytra, although the extent of this is not as great as that seen in tribe Trechini. This makes sense considering that almost all *Bembidion* species are capable of flight. In other cases a secondary doming of the elytra occurs as a derived character.

The pattern of striations on the elytra is much more varied than the general shape. Here the plesiomorphic state is what is seen in the *Bracteon*-group. Here there are eight similar striae which run uniformly from the base to the tip of the elytra; a ninth, finer stria is located directly on the edge. The eighth stria merges with the ninth in the front third; nearer the tip they are widely separated. Striae 1, 2, 5 or 7, along with 8 and 9 extend to the wing tip. The others are rather shortened and may unite. The eighth stria is only slightly more indented before the tip.

Subgenus *Pogonidium* shows the first stage in the development of the elytral striations, which is found in a number of other subgenera. The eighth stria is smoother, rather furrow-like rather than incised; the ninth stria is extremely fine and the eighth and ninth are separated by a very narrow but indented interval. The rest of the striae have the normal form and have clear punctures within them, separated by broad intervals.

The eighth stria has a rather different development in subgenus *Sinechostictus*. Here the front half of the stria is usually more or less faded and the interval between it and the ninth stria is often broader and not significantly indented. The rear section of the eighth stria is still clear, furrow-like and smooth.

B. moschatum has only the apical part of the eighth stria is developed (as in most *Sinechostictus* species) but towards the base it doesn't simply fade but it is fused in the rear third with the marginal stria which is deepened and furrow-like. In all other *Bembidion* species the 8th and 9th striae merge in the front third

Further evolutionary changes have occurred in the reduction of the elytral striae while the furrowed 8th stria has been retained. First the 7th striae becomes weaker until it completely disappears and then the same happens to the 6th and subsequent ones. At the same time the inner striae shorten; this means that the reduction occurs from the sides and from the tip. In many groups the apical parts of the 5th and 7th



striae are preserved and are referred to as the apical stria(e) (*Spitzenstreif(e)*). This is the same element that occurs genera *Tachys* and *Trechus* where the first stria is looped around at the tip and is linked to the apical of one of these striae.

Further reduction proceeds with the disappearance of the apical striae and of striae 2-5. In extreme cases (e.g. subgenus *Nepha*) only the sutural striae and the 8th striae remain, presumably to give some structural stiffness to the outer and inner margins of the elytra. The same sort of feature can be seen in subgenus *Phyla* and genus *Ocys* where there is a crease in the outer edge of the apical striae, which (as in *Trechus* and *Tachys*) curves around the tip of the elytra to the sutural striae.

b) punctures

Variation also occurs in the distribution of larger punctures on the elytra. Many Carabidae have a number of these on the elytra in different locations. Four rows of punctures may be recognised, along the 3rd, 5th, 7th and 9th striae. The one along the 9th stria has been termed the umbilical row by some authors. This row may be evenly spread along the entire length of the stria or more or less interrupted in the middle. The punctures along the inner striae are fewer in number and may be evenly distributed (as in the 3rd and 5th striae of *Calathus punctipennis* or the 7th striae of *Omphreus*) or only located in the apical part (e.g. in the 5th and 7th striae of *Harpalus dimidiatus*). These punctures may have a bristle arising from the centre (bristle-bearing punctures) or may not (pore-punctures).

In *Bembidion* the number of bristle-bearing punctures is considerably reduced. Apart from a few exceptions there are two punctures on or near the 3rd stria and one in the 5th. No punctures are present in the 7th striae. There are several punctures in the umbilical row behind the shoulders and near the tip. The two punctures associated with the 3rd striae are either located on the 3rd elytral interval (e.g. subgenera *Chrysobracteon*, *Pogonidium* and *Notaphus*) or on the stria (e.g. genus *Bracteon* and subgenera *Ocydromus* and *Plataphus*). These may be referred to as the dorsal punctures. The puncture on the 5th stria may be termed the preapical puncture because it is always close to the apical striae or is located within them. In cases where the apical striae are greatly indented, the preapical puncture may be indistinct and when the apical striae are absent, the preapical puncture is very clear and isolated.

Further reduction in the punctures is only found in some *Ocys* species (*harpaloides*, *berytensis*) in which there is only one dorsal puncture.

The plesiomorphic state is regarded as bristles and punctures small and simple. The deepening of the punctures (*Bracteon foraminosum*, subgenera *Testedium* and *Testediolum*) is regarded as secondary.

c) basal border and clavicular ridge

The basal border of the elytra is also of phylogenetic importance. In genus *Pogonus* (regarded as closest to the *Bembidion* archetype) the basal margin is an evenly concave curve extending from the short shoulder angle to the scutellum. In genus *Bembidion* it is interrupted in the middle, reaching from the shoulders at most to the



4th striae. There is then a tendency for the shoulder angle to become less acute and this is associated with a smoothing of the basal border until it is no longer distinct. The acute shoulder angle is seen in subgenera *Serrula*, *Pogonidium* and *Chlorodium*. It is obtuse in *Metallina lampros* and *Phyla obtusum* and then rounded in *Plataphodes fellmanni* and *Ocys harpaloides*. In other *Bembidion* species the shoulder angle is absent and the front margin of the elytra evenly curves onto the sides.

The clavicular ridge is located inside the inwardly curved margin of the shoulder and is often visible as a continuation of it. Its location and examination has proved to be difficult without experience due to its small size and its position. It may be necessary to remove the pronotum from the elytra and then examine the basal part of the elytra obliquely from the front. In most species of subgenera *Bembidion*, *Emphanes* and *Trepanes* this is an oblique ridge that turns slightly downwards and forwards, running from the shoulder to the side of the mesosternal stem, bordered dorsally by a sharply indented line. Ventrally this ridge curves directly onto the epipleuron.

This ridge can also be found in many species of *Trechus* which have obliquely convergent shoulder margins. In some species of *Dyschirius* (*strumosus*, *extensus*, *angustatus*) it has been long-recognised but incorrectly interpreted as the basal border. Netolitzky was the first to report it from genus *Bembidion* and named it the *crista clavicularis*. In *Bembidion* there is a true basal border which separates the dorsal striated part from the smooth basal area while the clavicular fold lies further forward and below, forming the boundary between the smooth basal area and the epipleura of the elytra.

The presence of the clavicular ridge is a derived character and is only present in species which no longer have a clear basal margin. Calling this the basal margin may appear justified from a physiological point of view but this would not be true according to comparative morphology.

Subgenus *Serrula* shows another feature of the elytra not seen in other groups. In other groups the sides of the elytra are uniformly smooth while in *Serrula* the margin is finely serrated and has minute hairs. This feature is also seen in some blind species of *Trechus* (particular in some from southern France).

Process of the metasternum

The underside shows a few characters of systematic interest. The most important is the structure of some parts of the metasternum, which extends between the middle coxae. This intercoxal process of the metasternum is bordered or not; in some species the border is only seen on the sides (along the inner edge of the coxae) or extends around the tip, where it is often more strongly incised. In forms with the rectangular pronotum and distinct shoulder angle, the metasternal process lacks a border at least at the tip; only in more derived types is a complete margin present.

Underside of the abdomen

The abdomen almost always has the two normal bristle-bearing punctures near the hind margin of each segment. The presence of a complete row of setae is a derived



feature, also occurring in other Carabidae such as *Laemostenus schmidtii*, *L. cavicolca*, *Trechus longicornis* and *T. globulipennis*.

Microscopic surface sculpture

The upper surface may have a microscopic surface sculpture and this has been studied by Netolitzky. He identifies four different types but they transition into one another:

- isodiametric reticulation in which the sculptural elements are about as long as wide
- broad transverse reticulation where the width of the elements is up to three times longer than their longitudinal length
- narrowly transverse reticulation where the width is more than three times longer than the length
- transverse wrinkles where the reticulation has become so narrow that the enclosed elements can no longer be seen

The isodiametric reticulation is regarded as the original form as it is seen in the least modified groups (genus *Bracteon*, subgenera *Serrula* and *Chlorodium*).

Microscopic sculpture may be lacking progressively first from the top of the pronotum, then from the sides, and finally from the elytra. The sculpturing is sometimes weaker in males than in females. The sculpture requires examination with a microscope but is generally clear enough. In groups with a dull sheen on the upper surface the very coarse isodiametric reticulation can be seen using a hand lens (genus *Bracteon*, subgenus *Chlorodium* etc). It should not be assumed that the surface sculpture is the same everywhere – the reticulation on the pronotum is often completely different from that on the elytra.

A detailed study of the coloration has already been done by Netolitzky. The markings in subgenera *Nepha* and *Bembidion* are sharply defined. There are often four paler patches on the elytra, two shoulder patches and two preapical patches. In others the basal part or the apical part of the elytra is generally pale. Darker legs and antennae are hypothesised as plesiomorphic with tendencies for the antennae to become paler towards the base, paler femora and tibiae being derived.



Phylogeny and subgenus groupings

There is no doubt that genus *Bracteon* and subgenus *Chrysobracteon* are the most primitive. Both have the following plesiomorphic characters:

- two undivided parallel frontal furrows
- broad and flattened pronotum
- angular shoulders with a short basal border
- unbordered metasternal process
- upper surface with a uniform reticulate microscopic sculpture
- complete striae on the elytra

The derived characters are:

- ridges by the hind angles of the pronotum weak or absent
- presence of mirror-spots on the elytra
- reduction of the front marginal bristle on the pronotum

Subgenus *Serrula* is similar to the above in the head and pronotum features but has the 8th striae more strongly incised and the margin of the elytra finely serrated.

Subgenus *Notaphus* is closely related to *Chrysobracteon* according to Netolitzky but has the basal margin of the elytra absent and a deepened 8th stria on the elytra. Like this subgenus, *Notaphus* has the dorsal punctures in the third interval of the elytra.

Subgenera *Omotaphus* and *Notaphocampa* are more highly differentiated. The clavicular ridge is present and the frontal furrows converge onto the front margin of the clypeus. Subgenera *Semicampa* and *Diplocampa* also have the dorsal punctures in the third interval of the elytra.

Subgenera *Pogonidium*, *Chlorodium*, *Neja* and *Metallina* form another series in which the basal margin of the elytra is clearly raised, the shoulders are angular. The dorsal punctures are usually in the third interval on the elytra although this may be debateable. In spite of their clear differences, the close relationship between *Pogonidium laticolle* and *Metallina lampros* is clear and the subgenera show a gradual change in characters.

Subgenus *Philochthus* is probably derived from the *Notaphus*-series, agreeing in the position of the dorsal punctures on the elytra. It has followed a different direction in the form of the pronotum. The frontal furrows have remained primitive. It has reduced striations on the elytra and a clear clavicular ridge.

Subgenera *Phyla*, *Ocys* and *Oreocys* have in common

- keel-like outer edge of the apical striae
- dorsal punctures clearly in the third interval
- sides of the pronotum not always clearly convex in front of the hind angles

Subgenera *Plataphodes*, *Plataphus*, *Ocydromus* and *Nepha* form another related group with their most primitive members similar in shape, structure of the pronotum and striation of the elytra to *Notaphus*. The most derived of the group (*Nepha*) are similar to subgenus *Bembidion*. From both they are differentiated by the position of



the dorsal punctures in the third striae. From subgenus *Bembidion* they also differ in that the frontal furrows do not converge onto the clypeus.

Subgenus *Plataphodes* has primitive characters which also occur in the *Ocydromus*-group –

- the pronotum is flattened with postangular ridges,
- completely striated elytra with a basal margin and almost angled shoulders
- metasternal process unbordered towards the tip
- upper surface with a reticulate sculpture all over
- uniformly dark metallic colour

Plataphus is derived from *Plataphodes* through a reduction of the basal margin of the elytra.

Subgenus *Bembidionetolitzkya* is related to *Plataphus* but is not clearly differentiated from subgenus *Ocydromus*. The pronotum has the primitive shape. The striations on the elytra are weakened towards the margins and the metasternal process is completely bordered. The upper surface is completely reticulate as in *Plataphus*, or at most the middle part of the pronotum may be smooth.

Subgenus *Nepha* shows the greatest level of development in the pronotum (strongly heart-shaped and convex in section) and the elytral striations show the greatest reduction. The upper surface is almost always smooth and the elytra have well-defined colour patterns.

Subgenera *Sinechostictus*, *Pseudolimnaeum* and *Limnaeum* are close to the *Bembidionetolitzkya/Ocydromus* group, sharing the position of the dorsal punctures on the elytra. *Sinechostictus* and *Pseudolimnaeum* are more closely related to each other as they lack the border on the metasternal process and have clearly punctured lateral parts of the mesothorax. *Limnaeum* is more isolated in the group which has complete striations on the elytra but has reduced eyes and in one species (*nigropiceum*) has become wingless; the process of the metasternum is bordered.

A further small group includes the very closely-related subgenera ***Princidium* and *Actedium***. *Princidium* includes dark-coloured and more primitive species with complete striation on the elytra. *Actedium* species are paler species of coastal habitats with reduced striae on the elytra leaving the preapical puncture isolated. Both have a fairly derived pronotal structure and have the lateral sections of the thorax punctured. Particularly noticeable is the coarse, wrinkled sculpture of the head and the weak, indistinct frontal furrows. Some features of *Princidium* (the punctures on the thorax, the form of the pronotum, the course of the 8th striae and overall appearance) are reminiscent of the more primitive *Sinechostictus* species (*cribrum* and *dahl*).

Subgenus *Testedium* has a similar sculpturing on the head as *Princidium* and *Actedium* but the exact location of the dorsal punctures is difficult to assess due to their enlarged size.

Subgenera *Talanes*, *Emphanes* and *Bembidion* form another series of species which share



- strongly heart-shaped and convex pronotum with narrow rather outwardly-directed basal impressions,
- metasternal process bordered
- preapical puncture isolated on the elytra
- dorsal punctures located in the 3rd interval.

Subgenus *Talanes* is the most primitive with the frontal furrows parallel, the elytra with a clear microsculpture and lacking a clavicular ridge. The species of *Emphanes* have smooth elytra with a clavicular ridge and have the frontal furrows parallel to convergent. *Bembidion* has smooth elytra, a distinct clavicular ridge, convergent frontal furrows and the hind angles of the pronotum extended in a small tooth.

Subgenera *Trepanedoris* and *Trepanes* both have strongly convergent frontal furrows which almost appear to have a puncture where they meet at the front. *Trepanedoris* lacks a border on the metasternal process and lacks a clavicular ridge.

