

New beetle larvae (Coleoptera: Coptoclavidae, Caraboidea, Polyphaga) from the Upper Triassic of Germany

Новые личинки жуков (Coleoptera: Coptoclavidae, Caraboidea, Polyphaga) из верхнего триаса Германии

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КЛЮЧЕВЫЕ СЛОВА: Coleoptera, личинки, триас, Германия, Coptoclavidae, Caraboidea, Polyphaga, эволюция.

ABSTRACT. Three new larvae, †*Protonectes germanicus* **gen. et sp.n.**, †*Carabilarva triassica* **sp.n.**, and †*Larvula triassica* **sp.n.**, are described from the Triassic of Germany (Coburger Sandstein, Hassberge Formation, Middle Keuper). These taxa are the earliest known larvae of the family Coptoclavidae, subfamily Caraboidea, and suborder Polyphaga, respectively. The evolutionary changes of Coptoclavidae and all Dytiscoidea and life forms of the earliest known larvae of ground beetles (in the broad sense) are discussed.

РЕЗЮМЕ. Три новые личинки: †*Protonectes germanicus* **gen. et sp.n.**, †*Carabilarva triassica* **sp.n.**, †*Larvula triassica* **sp.n.** описаны из триаса Германии (Кобургский песчаник, свита Хасберге, средний кейпер). Данные таксоны являются наиболее древними из известных личинок семейства Coptoclavidae, надсемейства Caraboidea и подотряда Polyphaga, соответственно. В статье рассматриваются эволюционные преобразования личинок коптоклавид и дитискоидов в целом; жизненные формы древнейших личинок жужелиц (в широком в смысле).

Introduction

The Triassic insects of Germany are rare and rather poorly studied. The most abundant insect assemblage was discovered in the Upper Buntsandstein (Lower Anisian) of Lower Franconia [Bashkuev et al., 2012],

which is near-contemporaneous with a number of other assemblages known in European Triassic: the richest one occurs in the “Grès à Voltzia” Formation of the Vosges Mountains [Gall & Grauvogel-Stamm, 2005], the others are known from the Buntsandstein of Mallorca [Zessin, 2008] and from the Holy Cross Mountains in Poland [Żyła et al., 2013]. From the younger deposits of the Germanic Basin, only sparse and non-diverse insects have been described, mainly from the Lower and Upper Keuper (Rhaetian) [Geyer & Kelber, 1987; Brauckmann & Schlüter, 1993, and references cited there]. Quite recently, Barth et al. [2011] reported a diverse insect fauna from the new late Middle Keuper (Late Norian) fossil site at the nearby Langenberg, Lower Saxony, which is currently the richest Late Triassic insect fauna known in Germany. Among others, aquatic larvae of beetles were mentioned, but remain unstudied.

In addition, insect remains are known from the Middle Keuper Coburger Sandstein (Hassberge Formation, Upper Carnian) in Lower Franconia. The Coburger Sandstein crops out at numerous quarries in the Hassberge area and shows a remarkable interbedded succession of fluvial channel sandstones intercalated with fine-laminated lacustrine and floodplain sediments. The beds are rich in fossils [Kelber & Nitsch, 2005], including, besides insects, particularly abundant remains of *Triops cancriformis* [Kelber, 1999], as well as conchostracans, fish remains, thermo-

pod tracks, invertebrate ichnofossils, and diverse macroflora.

Insect remains collected in Coburger Sandstein (mainly from a quarry south of Eltmann) number several hundred specimens, mostly beetles [J. Sell, pers. comm. to A.S. Bashkuev, 2013], but all the material is housed in private collections and has never been studied by specialists. Only a few specimens were mentioned in publications: e.g., an odonate referred to as *Triadotypus* cf. *guillaumei* Grauvogel et Laurentiaux, 1952 [Bechly, 2013, in press] and a cupedoid elytron [Kelber in Reimann & Schmidt-Kaler, 2002: 16], which can be assigned to the genus *Zygadenia* Handlirsch, 1906.

A number of insect remains (about 40 specimens) were collected by Jürgen Sell (SMTE) and one of the authors (ASB) at the quarry Schönbachsmühle near Ebelsbach in 2012 and 2013. This collection includes fragments of orthopterans and cockroaches, single specimens of Thysanoptera, Trichoptera, and possible Raphidioptera, elytra of Cupedidae (not only *Zygadenia*, but also other morphotypes), and diverse larvae, including several well-preserved beetle larvae described herein. This collection includes also elytra similar in shape and dark coloration pattern to those of *Holcoptera* Handlirsch, 1906, known from the Triassic of Europe and North America. There are reasons to suggest that these elytra belong to coptocladid beetles. In addition, a beetle hindwing of members of Coptoclavidae have been found at this site. Characters, which support assignment this hind wings to Coptoclavidae are: straight and long vein Cu2, the basal position of the common base vertex branches CuP and AA1+2, as well as large, long and convex forward 2nd anal cell [Fedorenko, in press].

Material and methods

The newly described fossils are deposited in the collection “Sammlung Mainfränkische Trias” in Markt Euerdorf, Lower Franconia (SMTE). The fossils are preserved as impressions in laminated clayey shale of lacustrine genesis. Two larvae (SMTE 5930/1–65 A and B) are preserved on the same slab and somewhat overlapping: the head of the latter was uncovered after fine preparation of the pronotum of the coptocladid larva. The same slab contains also a mayfly nymph and several head shields of *Triops*.

Fossils used for comparison are deposited in the collections of the Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia (PIN) and Capital Normal University, Beijing, China (CNU). Collections of recent beetle larvae are deposited in the Papanin Institute for Biology of Inland Waters, Russian Academy of Sciences, Borok, Russia, and Moscow State Pedagogical University, Moscow, Russia.

Photographs of the fossils were taken with a Leica M165c stereomicroscope and Leica DFC420 camera.

Results

Descriptions of new taxa

Order Coleoptera
Suborder Adephaga
Superfamily Dytiscoidea

Family Coptoclavidae Ponomarenko, 1961

†*Protonectes* Prokin et Ponomarenko, **gen.n.**
Figs 1–7

TYPE SPECIES: †*Protonectes germanicus* **sp.n.**

DIAGNOSIS: Larva. Head somewhat wider than long, narrowing anteriorly of eyes, nasale not protruding anteriorly. Mandibles without retinaculum, with two cutting surfaces and blunt tab medially on outer margin. Epicranial suture narrow; frontal sutures weakly sinuate. Length of antenna equal to maximum head width. Head subequal in length to prothorax. Pronotum almost twice as long as meso- or metanotum. Tracheae without pronounced taenidia; commissures and connectives not visible; spiracles present in posterior part of mesothorax. Sparse swimming hairs present on femora of fore- and midlegs and tarsi of hindlegs. Raptorial forelegs almost as long as maximum body width; natatorial hindlegs twice as long as maximum body width.

COMPARISON: The new genus is especially similar in the body shape, level of “constructive perfection” of legs structure of †*Daohugounectes primitivus* Wang, Ponomarenko et Zhang, 2009 from the Middle Jurassic of China, and differs from it in the mandibles without retinaculum and with a blunt tab on outer margin, shorter epicranial suture, and sparser swimming hairs, which are absent on mesotibia, mesotarsus and metatibia. The new genus is also similar in the structure of thoracic apodemes to †*Stygeonectes jurassicus* Ponomarenko, 1977, and differs from it in the structure of mandibles and sparser swimming hairs of the legs. Comparison with the other known species of Mesozoic dytiscoid larvae and members of recent families is given below (table).

ETYMOLOGY: From traditional latinization of the Greek πρῶτος = *protos* (first) and the *nectes*, traditional latinization of the Greek νῆκτης = *nektes* (swimmer).

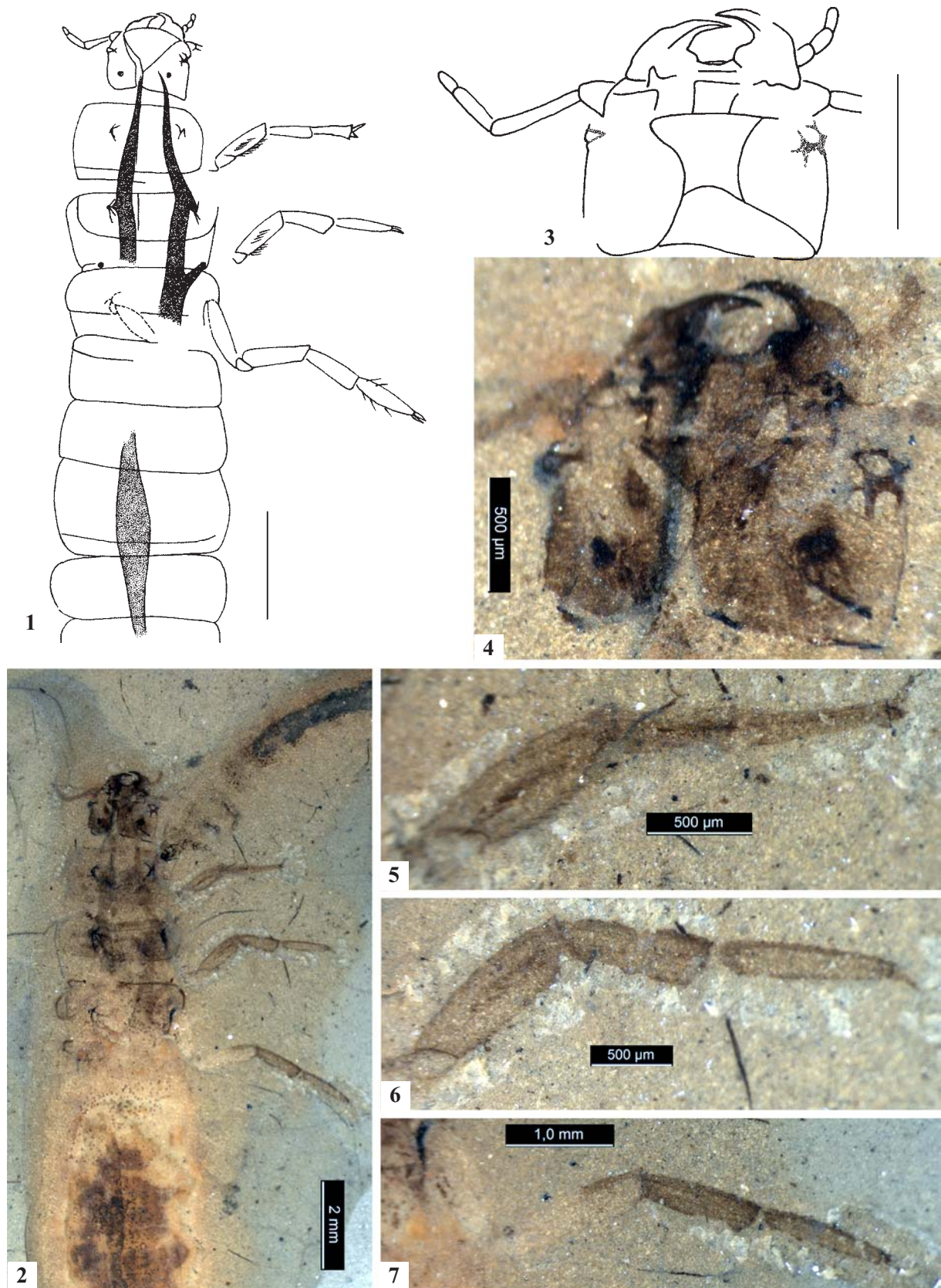
†*Protonectes germanicus* Prokin et Ponomarenko,
sp.n.
Figs 1–7

MATERIAL: Holotype SMTE 5930/1–65A, part and counterpart.

LOCALITY AND HORIZON. Quarry Schönbachsmühle near Ebelsbach, Lower Franconia; Coburger Sandstein, Hassberge Formation, Middle Keuper, Upper Carnian.

DESCRIPTION (Figs 1–2, 5–9). Medium-sized larva, with incompletely preserved abdomen. Body terete, widest at level of abdominal segments 3 and 4. Antennomere 2 longer than antennomeres 3 and 4 together; antennomere 3 three times as long as antennomere 4; antennomere 1 wider than long, twice as wide as any other antennomere. Maxillary palpus with homonomous palpomeres and equal in length to mandible. Ocelli at boundary between anterior and medial third of head; ocellar tubercles almost not protruding. Tibiae and tarsi of all pairs of legs subequal in length.

MEASUREMENTS: Total length of impression 11.8 mm; taking into account the incompletely preserved abdomen, body length without urogomphi was probably about 16 mm. Maximum body width (at level of abdominal segments 3 and 4) 3.4 mm. Length of head, pro-, meso- and metathorax (including not only the sclerotized tergite, but also the poste-



Figs 1–7. †*Protonectes germanicus* gen. et sp.n., holotype: 1–2 — general view; 3–4 — head; 5 — foreleg; 6 — midleg; 7 — hindleg; scale bars: 1 — 2 mm; 3 — 1 mm.

Рис. 1–7. †*Protonectes germanicus* gen. et sp.n., голотип: 1–2 — общий вид; 3–4 — голова; 5 — передняя нога; 6 — средняя нога; 7 — задняя нога; масштаб: 1 — 2 мм; 3 — 1 мм.

rior membranous part) 1.4 mm. Head width 1.5 mm; prothorax width 2.5 mm; meso- and metathorax width 2.9 mm. Hindleg length 5.3 mm.

ETYMOLOGY: From Germany.

Superfamily Caraboidea

Formal genus †*Carabilarva* Ponomarenko, 1985

†*Carabilarva triassica* Makarov et Prokin, **sp.n.**

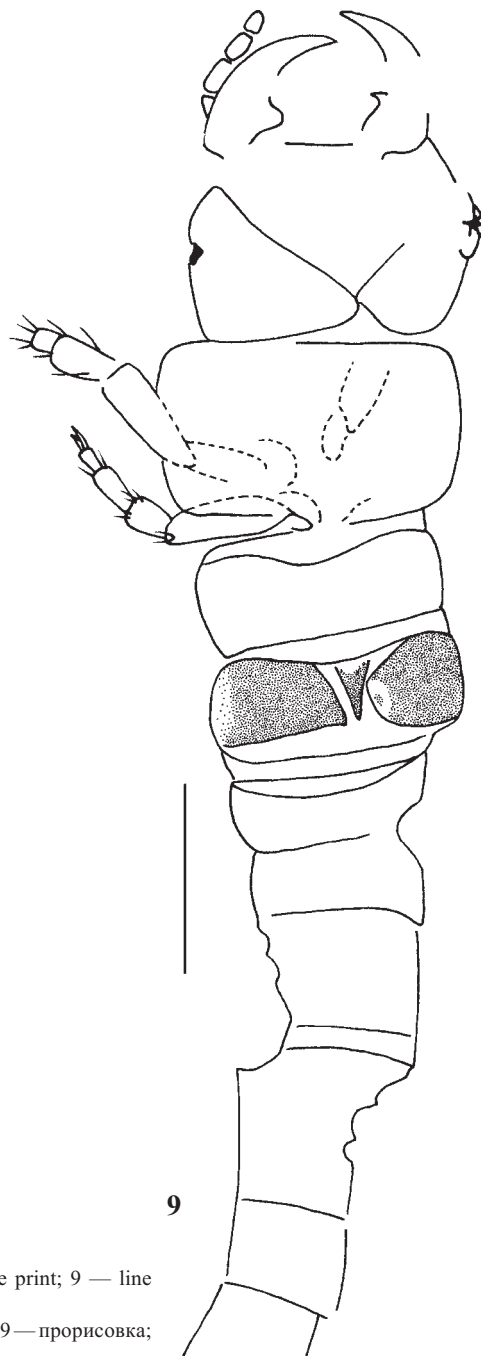
Figs 8–13

MATERIAL: Holotype SMTE 5930/1–63; part and counterpart.

LOCALITY AND HORIZON. Quarry Schönbachsmühle near Ebelsbach, Lower Franconia; Coburger Sandstein, Hassberge Formation, Middle Keuper, Upper Carnian.

DESCRIPTION (Figs 3–4, 10–13). Larva with incompletely preserved abdomen: only six proximal segments present. Head capsule wide, wider than long, with occipital area visibly narrowing towards posterior margin of head. Epicranial suture short, barely discernible; frontal sutures weakly sinuate in area of dorsal tentorial foveae. Ocellar tubercles protruding, positioned in anterior third of epicranial sclerite, with six ocelli each. Epicranial sclerites with traces of punctation and of rugose sculpture.

Antenna 4-segmented; antennomere 2 longer than any other antennomeres. Nasale poorly discernible, without distinct teeth, shape of its anterior margin indiscernible, lying visibly proximal to level of anterior angles of paraclypeus. Mandibles with large retinaculum, weakly curved posteri-



Figs 8–9. †*Carabilarva triassica* **sp.n.**, holotype, general view: 8 — positive print; 9 — line drawings; 13 — counterprint, details of head; scale bar: 9 — 1 mm.

Рис. 8–9. †*Carabilarva triassica* **sp.n.**, голотип, внешний вид: 8 — отпечаток; 9 — прорисовка; масштаб: 9 — 1 мм.

ad, pointed, positioned at boundary between basal and medial third of mandible. Labium with large, strongly protruding, sclerotized ligula. Judging by shape of distal part of ligula, it bore three large setae, set widely apart. Pronotum trapezoid, with maximum width near anterior margin, with distinct wide pretergite. Meso- and metanotum considerably shorter than pronotum, considerably wider than long, with transverse carina, separating pretergite, preserved on metanotum. Legs with trochanters and femora elongate; femur and tibia with apical groups of spine-like setae. Tarsus with two subequal claws. Abdominal tergites distinctly wider than long. Small punctation discernible on thoracic and abdominal tergites.

MEASUREMENTS: Length of impression 7.2 mm; taking into account the incompletely preserved abdomen, total body length was probably about 9.2 mm. Length of head (with mandibles) 1.7 mm; pronotum length 0.9 mm; meso- and metanotum length 0.5 mm. Maximum head width 1.7 mm; maximum pronotum width 1.6 mm; maximum meso- and metanotum width 1.3 mm.

COMPARISON: The new species differs from †*Carabilarva jurassica* Ponomarenko, 1985 and †*Carabilarva robusta* Makarov, 1995 in the smaller size, relatively large head dilating anteriorly, and retinaculum shifted towards the base of the mandibles. In addition, the new species differs from †*C. robusta* in the considerably shorter epicranial suture.

ETYMOLOGY: From the Triassic period.

Suborder Polyphaga

Familia incertae sedis

Formal genus †*Larvula* Ponomarenko, 1985

†*Larvula triassica* Prokin et Ponomarenko, **sp.n.**

Figs 14–17.

MATERIAL: Holotype SMTE 5930/1–65B, part and counterpart; paratype SMTE 5930/1–120 (A, B), part of two larvae and counterpart of one.

LOCALITY AND HORIZON. Quarry Schönbachsmühle near Ebelsbach, Lower Franconia; Coburger Sandstein, Hassberge Formation, Middle Keuper, Upper Carnian.



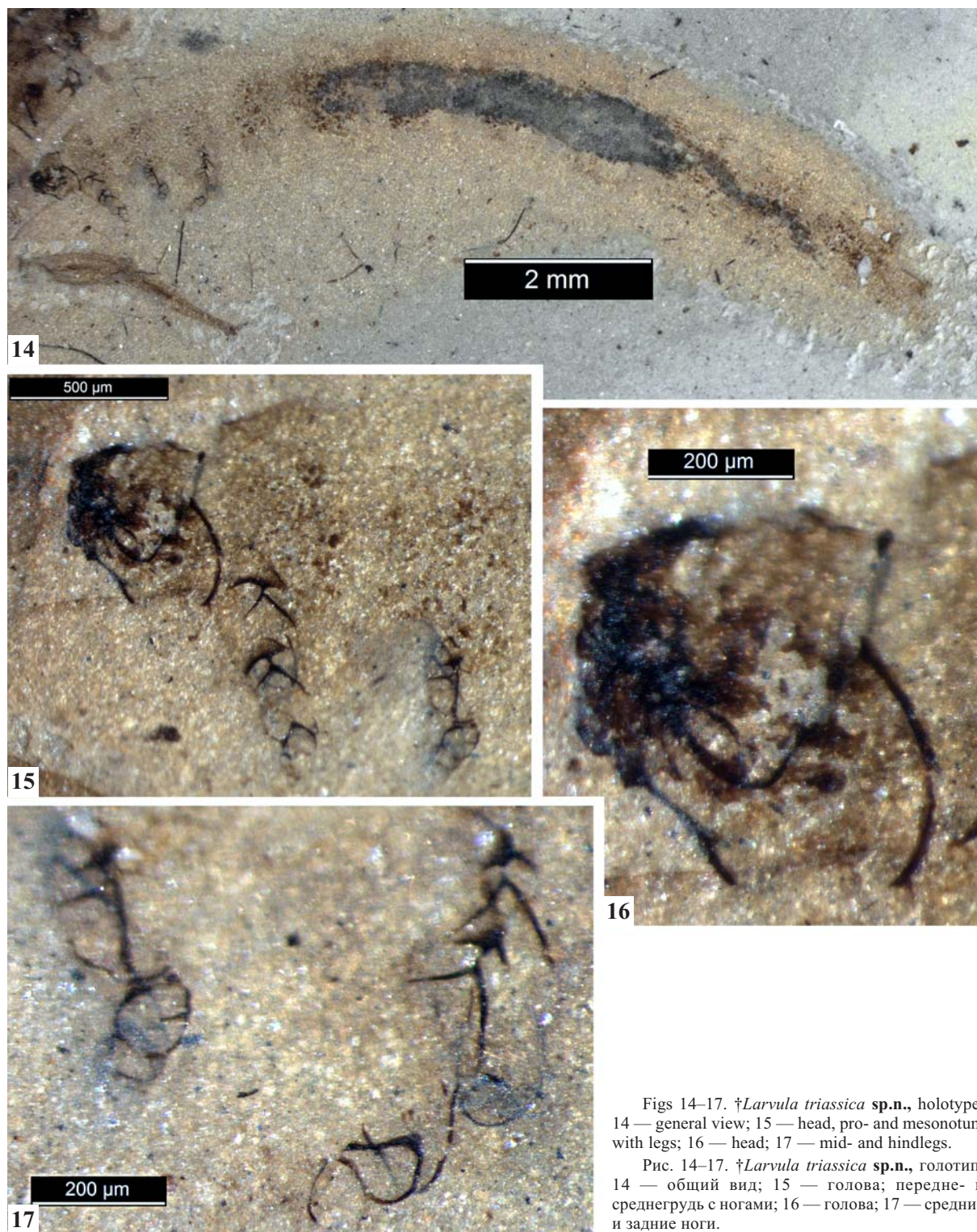
Figs 10–13. †*Carabilarva triassica* **sp.n.**, holotype: 10 — positive print, details of legs; 11 — counterprint, head and thorax; 12 — counterprint, head, 13 — head, line drawing; scale bar — 0.5 mm.

Рис. 10–13. †*Carabilarva triassica* **sp.n.**, голотип: 10 — прямой отпечаток, детали строения ноги; 11 — обратный отпечаток, голова и грудь; 12 — обратный отпечаток, голова; 13 — прорисовка строения головы; масштаб: 0,5 мм.

DESCRIPTION (Figs 14–17). Small elongate larva, rounded in cross-section, with partially retractable head and very weak or totally absent sclerotization of tergites of thoracic and abdominal segments. Number of abdominal segments at least nine; posterior end of body not preserved. Thoracic segments somewhat shorter than abdominal segments; spiracles not discernible. Gut occupying at least 1/3 of body height, discernible along abdominal segments 2 to 8. Legs 5-segmented (with

tibiotarsus). Femur longer than tibiotarsus; coxa subequal in length to femur; trochanter relatively short. Legs at least half as long as height of thoracic segments.

MEASUREMENTS: Length of preserved portion of body 10.2 mm; taking into account the possible presence of another abdominal segment, total body length was probably about 11.2–11.5 mm. Maximum height of abdominal segment (at level of segment 4) 1.6 mm.



Figs 14–17. †*Larvula triassica* sp.n., holotype: 14 — general view; 15 — head, pro- and mesonotum with legs; 16 — head; 17 — mid- and hindlegs.

Рис. 14–17. †*Larvula triassica* sp.n., голотип: 14 — общий вид; 15 — голова; передне- и среднегрудь с ногами; 16 — голова; 17 — средние и задние ноги.

COMPARISON: The new species differs from †*Larvula crassa* Ponomarenko, 1985 in the non-flattened body shape, less wide head with non-protruding ocellar tubercles and antennae, absence of sclerotization in thoracic segments, and twice as great total length.

ETYMOLOGY: From Triassic period.

Discussion

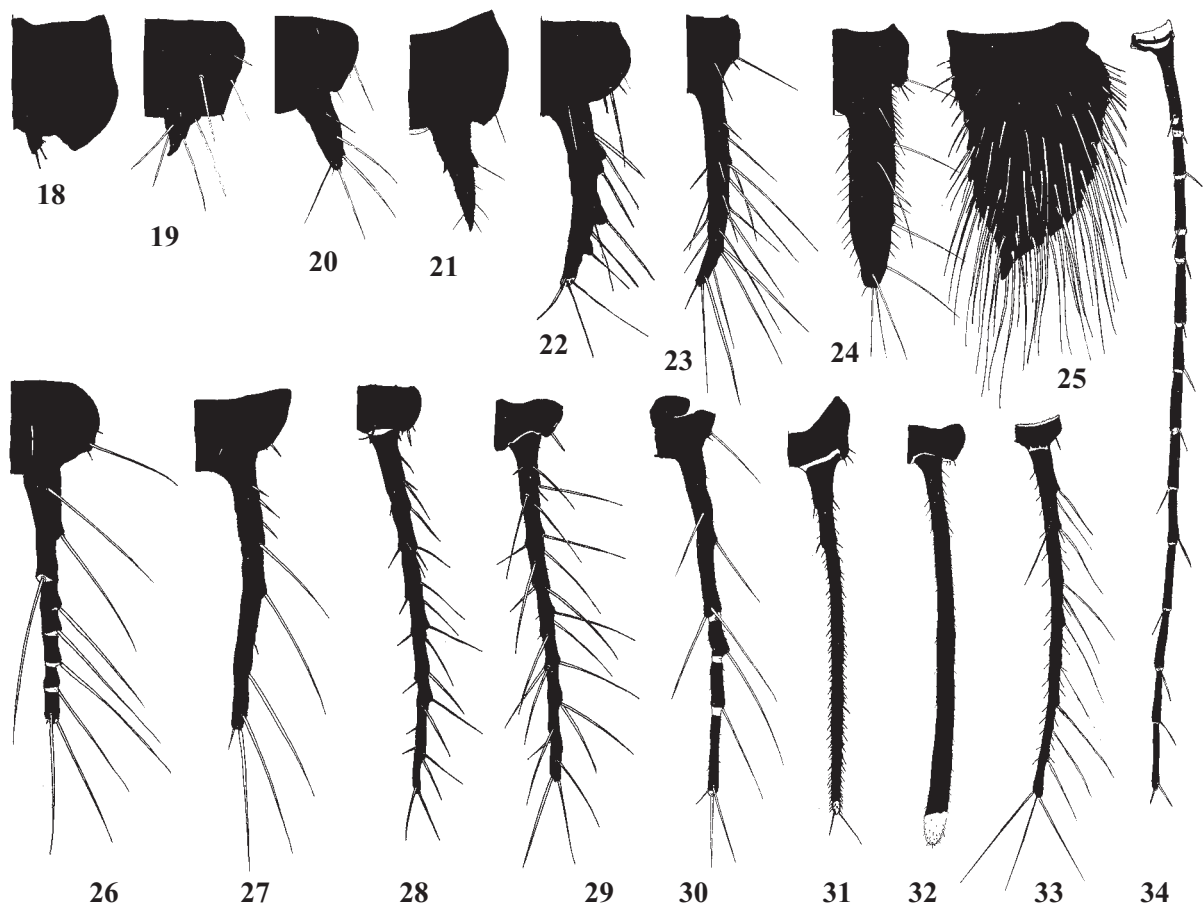
Three larval synapomorphies of Dytiscoidea are known [Alarie et al., 2004]: (1) abdominal segment 9 strongly reduced in size; (2) abdominal segment 10 absent or extremely reduced; (3) enlarged, terminal spiracles of abdominal segment 8.

All these apomorphies are not absolute. The spiracles of abdominal segment 8 do not function in 3rd instar larvae of *Noterus*, and, by contrast, in mature larvae of Dytiscidae

(judging by the structure of the spiracles, it was also true of Coptoclavidae) the spiracles of mesothorax and abdominal segments 1 to 7 function prior to pupation.

In the discussion of the structure of the larval †*Daohugounectes primitivus* Wang, Ponomarenko et Zhang, 2009, the following characters were indicated as plesiomorphic for this genus: (1) preserved vestige of nasale; (2) elongate mandible with only two teeth; (3) mid- and hindlegs changed for swimming not so strongly as in other coptooclavids; (4) relatively weakly developed taenidia of main tracheae; and (5) preserved vestige of abdominal segment 9 [Wang et al., 2009].

The complete reduction of the terminal abdominal segments in Dytiscoidea raises doubts, since a “derivative of abdominal segment 9” (sensu Wang et al., [2009]) is present in almost all known larvae of Coptoclavidae, as well as in Parahygrobiiidae and Aspitytidae (table). In the best studied of the listed species, †*C. longipoda*, this structure is not

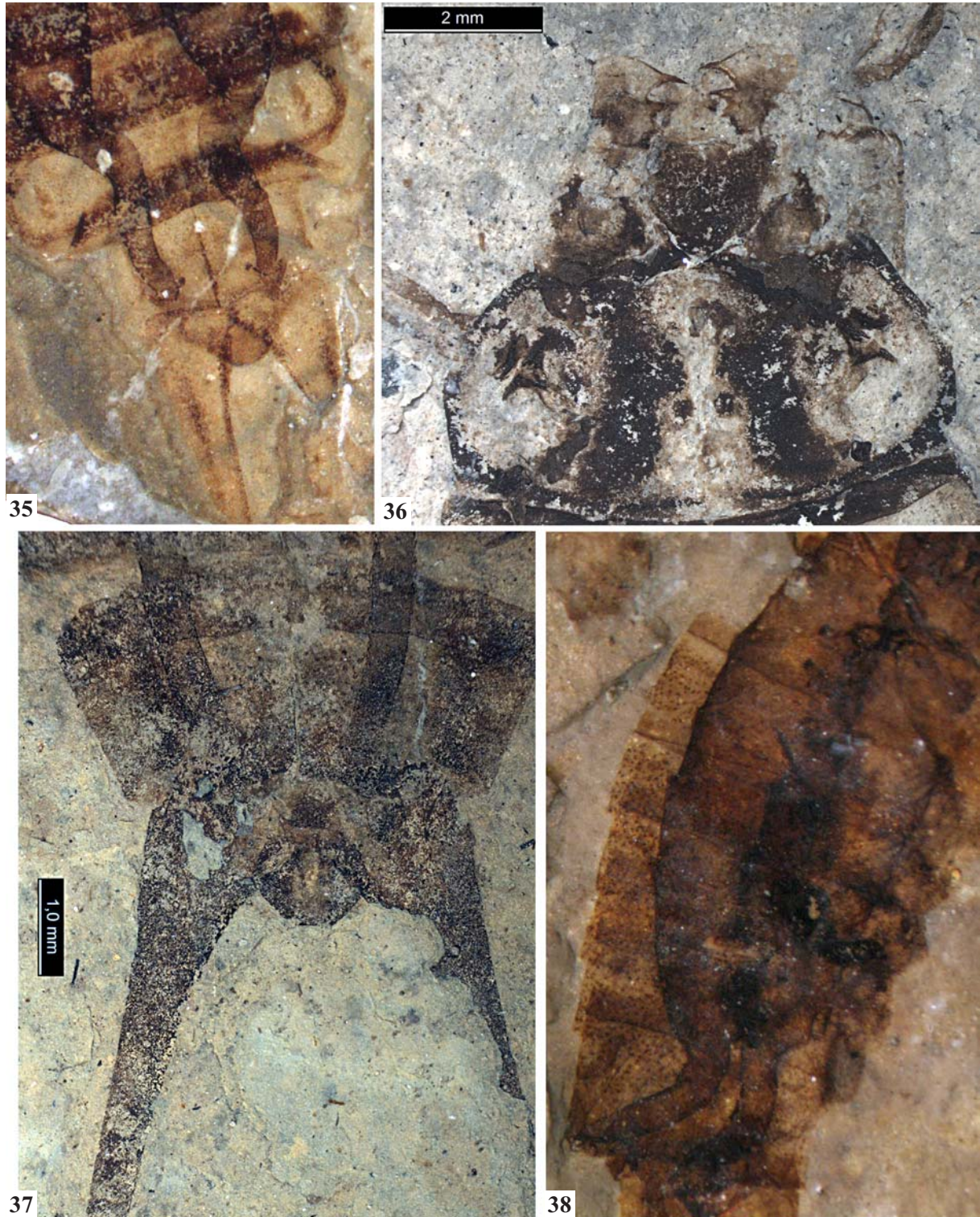


Figs 18–34. The aspect ratio of tergite IX and urogomphi in the family Carabidae: 18 — *Cychrus caraboides* (Linné, 1758); 19 — *Trachypachus holmbergi* Mannerheim, 1853; 20 — *Paradromius (Manodromius) linearis* (Olivier, 1795); 21 — *Carabus* (s.str.) *granulatus* Linné, 1758; 22 — *Diacheila fausti* Heyden, 1887; 23 — *Omophron* (s.str.) *limbatum* (Fabricius, 1777); 24 — *Clivina* (s.str.) *fossor* (Linné, 1758); 25 — *Anthia* (s.str.) *mannerheimii* Chaudoir, 1842; 26 — *Agonum (Olisares) mandli* Jedlička, 1933; 27 — *Oodes (Oodes) helopioides* (Fabricius, 1792); 28 — *Pelophila borealis* (Paykull, 1790); 29 — *Nebria (Boreonebria) frigida* R.Sahlberg, 1844; 30 — *Odacantha* (s.str.) *melanura* (Linné, 1767); 31 — *Callistus lunatus* (Fabricius, 1775); 32 — *Panagaeus* (s.str.) *cruxmajor* (Linné, 1758); 33 — *Loricera* (s.str.) *pilicornis* (F. 1775); 34 — *Drypta* (s.str.) *dentata* (P.Rossi 1790).

Рис. 18–34. Соотношение размеров IX тергита и урогомф в семействе Carabidae: 18 — *Cychrus caraboides* (Linné, 1758); 19 — *Trachypachus holmbergi* Mannerheim, 1853; 20 — *Paradromius (Manodromius) linearis* (Olivier, 1795); 21 — *Carabus* (s.str.) *granulatus* Linné, 1758; 22 — *Diacheila fausti* Heyden, 1887; 23 — *Omophron* (s.str.) *limbatum* (Fabricius, 1777); 24 — *Clivina* (s.str.) *fossor* (Linné, 1758); 25 — *Anthia* (s.str.) *mannerheimii* Chaudoir, 1842; 26 — *Agonum (Olisares) mandli* Jedlička, 1933; 27 — *Oodes (Oodes) helopioides* (Fabricius, 1792); 28 — *Pelophila borealis* (Paykull, 1790); 29 — *Nebria (Boreonebria) frigida* R.Sahlberg, 1844; 30 — *Odacantha* (s.str.) *melanura* (Linné, 1767); 31 — *Callistus lunatus* (Fabricius, 1775); 32 — *Panagaeus* (s.str.) *cruxmajor* (Linné, 1758); 33 — *Loricera* (s.str.) *pilicornis* (F. 1775); 34 — *Drypta* (s.str.) *dentata* (P.Rossi 1790).

always discernible in impressions, but Ponomarenko [1961] in his justification of the placement of this larvae in the order Coleoptera indicated it in fig. 5 (p. 70).

Comparison of the relative size and position of terminal segments of aquatic larvae of different coleopteran families that have only one pair of functional spiracles preserved on

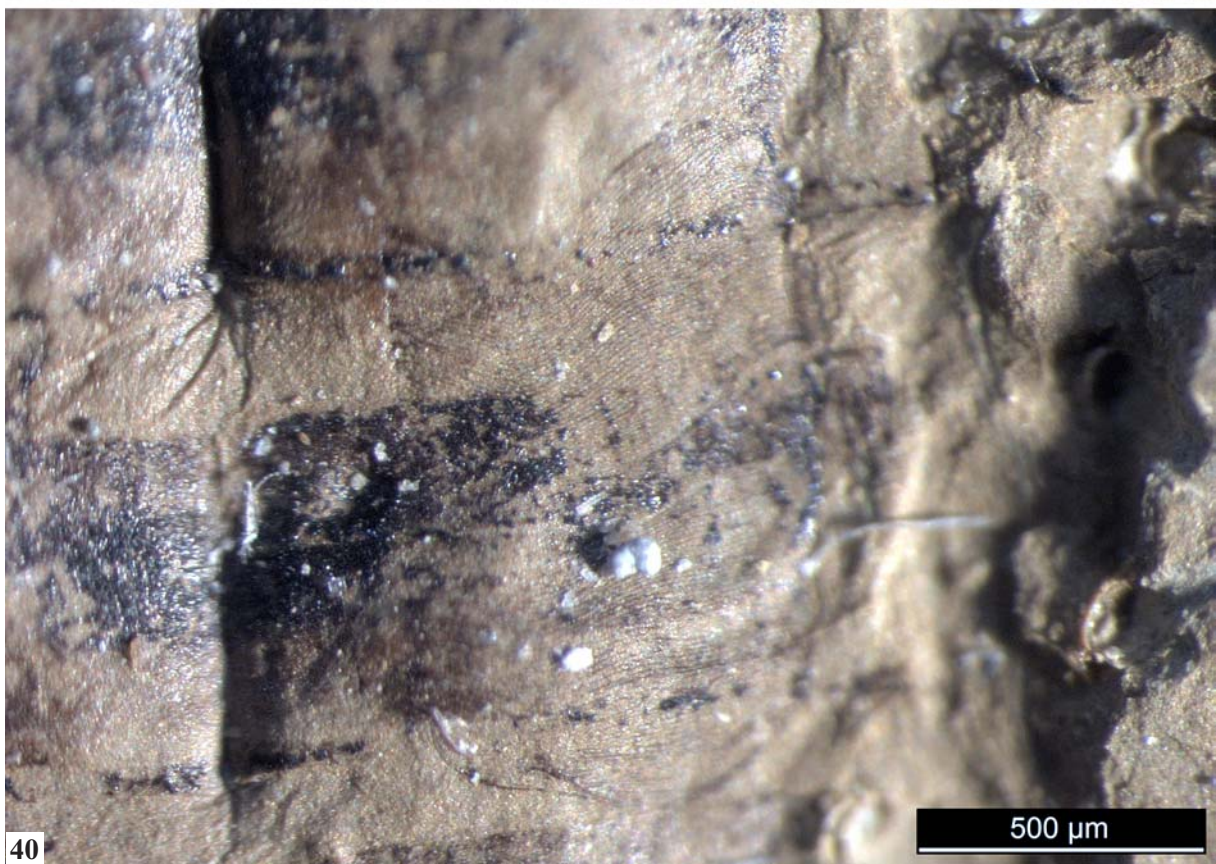


Figs 35–38. †*Coptoclava longipoda* Ping, 1928: 35–37 — body apex; 38 — head; 35, 37 — dorsal view; 36 — lateral view; 35 — CNU2009047 [Yixian Formation, China]; 36 — CNU 2009015 [Yixian Formation, China]; 37 — PIN 5026/918 [Khasurty, Lower Cretaceous, Transbaikalia]; 38 — PIN 3064/748 [Baissa, Lower Cretaceous, Transbaikalia].

Рис. 35–38. †*Coptoclava longipoda* Ping, 1928: 35–37 — вершина брюшка; 38 — голова и переднеспинка; 35, 37 — сверху; 36 — сбоку; 35 — CNU2009047 [Yixian Formation, China]; 36 — CNU 2009015 [Yixian Formation, China]; 37 — PIN 5026/918 [Khasurty, Lower Cretaceous, Transbaikalia]; 38 — PIN 3064/748 [Baissa, Lower Cretaceous, Transbaikalia].

abdominal segment 8 shows a similar pattern of morphological changes: in all cases, strong reduction of abdominal segment 10 and less considerable reduction of segment 9 are observed, with the ventral parts of these segments becoming

reduced first. In some cases (Meruidae and Hydrophilidae) this reduction is accompanied by enlargement of the sternite of segment 8; in others (Amphizoidae, Dytiscidae, Noteridae and Aspidytidae) the relative size of the tergite and sternite of



Figs 39–40. †*Colymbotethis antecessor* Ponomarenko, 1993: 39 — general view; 40 — spiral thickening of the tracheae; 39 — PIN2497/14; 40 — PIN2497/11.

Рис. 39–40. †*Colymbotethis antecessor* Ponomarenko, 1993: 39 — общий вид; 40 — спиральное утолщение стенки трахеи; 39 — PIN2497/14; 40 — PIN2497/11.

segment 8 remain unchanged. As a result, in Dytiscidae a dorsal fold is all that remains of segment 10, with longitudinal intersegmental muscles attached to this fold [Speyer, 1922]. In spite of the strong reduction, all main topological ratios between structures of terminal segments (the anus, urogomphi, etc.) remain unchanged.

The degree of reduction of tergite 9 can vary: it is well-developed in Meruidae, preserved as a rather small sclerite in Dytiscidae and Noteridae, and entirely lost in Amphizoidae (in the latter case the base of the urogomphi is dilated and, in essence, represents the dorsal surface of segment 9). At least in Dytiscidae [Speyer, 1922] no less than four pairs of muscles are connected to the base of the urogomphi; two of these pairs begin at the anterior margin of tergite 8 and thus correspond to

ordinary longitudinal intersegmental muscles. This means that in the larvae of Dytiscidae remnants of tergite 9 participate in the formation of the basal portion of the urogomphi.

It has to be noted that among Carabidae (Figs 18–34) a similar morphological trend is clearly traceable: as the urogomphi increase in size, and especially as they become mobile, the area of tergite 9 considerably diminishes, up to the transformation of this tergite into a rather small semicircle at the base of the urogomphi. Hence, the presence of larval urogomphi already implies that segment 9 is preserved.

Therefore, the structure visible in Coptoclauidae, Parahydrobiidae and Aspidytidae and lying ventrally relative to the base of the urogomphi should be interpreted as abdominal segment 10, rather than 9 [as it was incorrectly interpreted by



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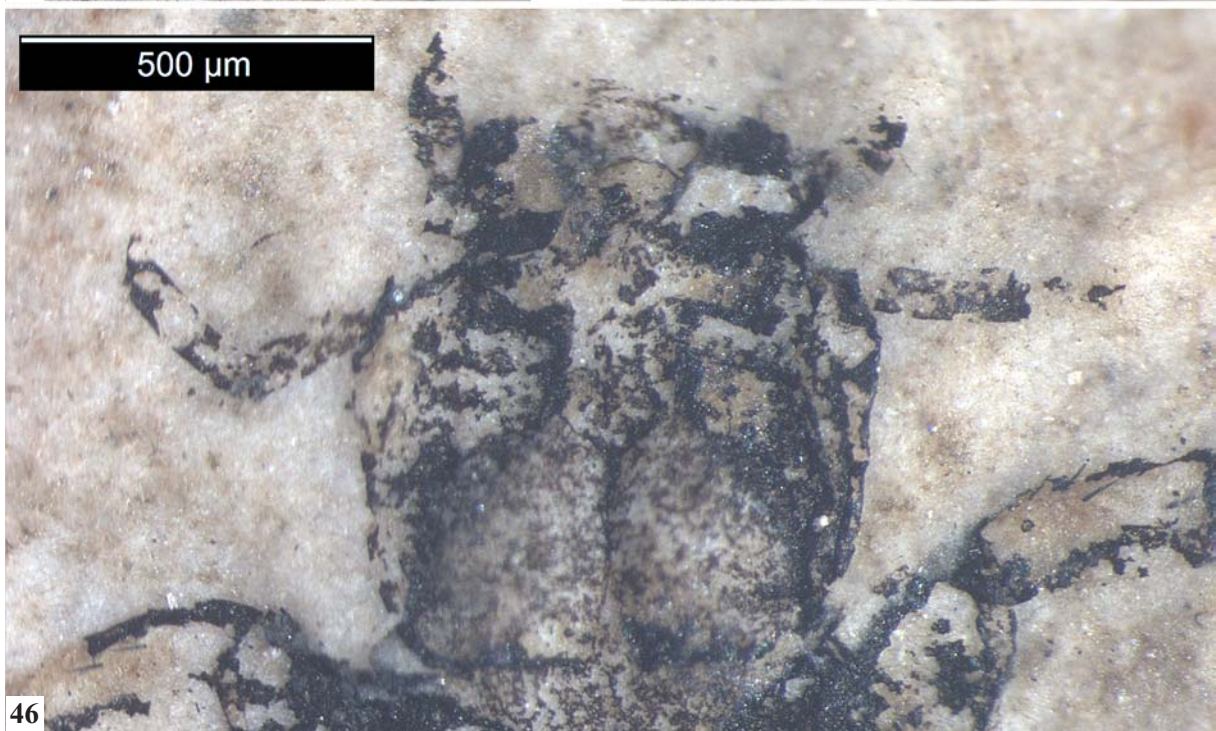
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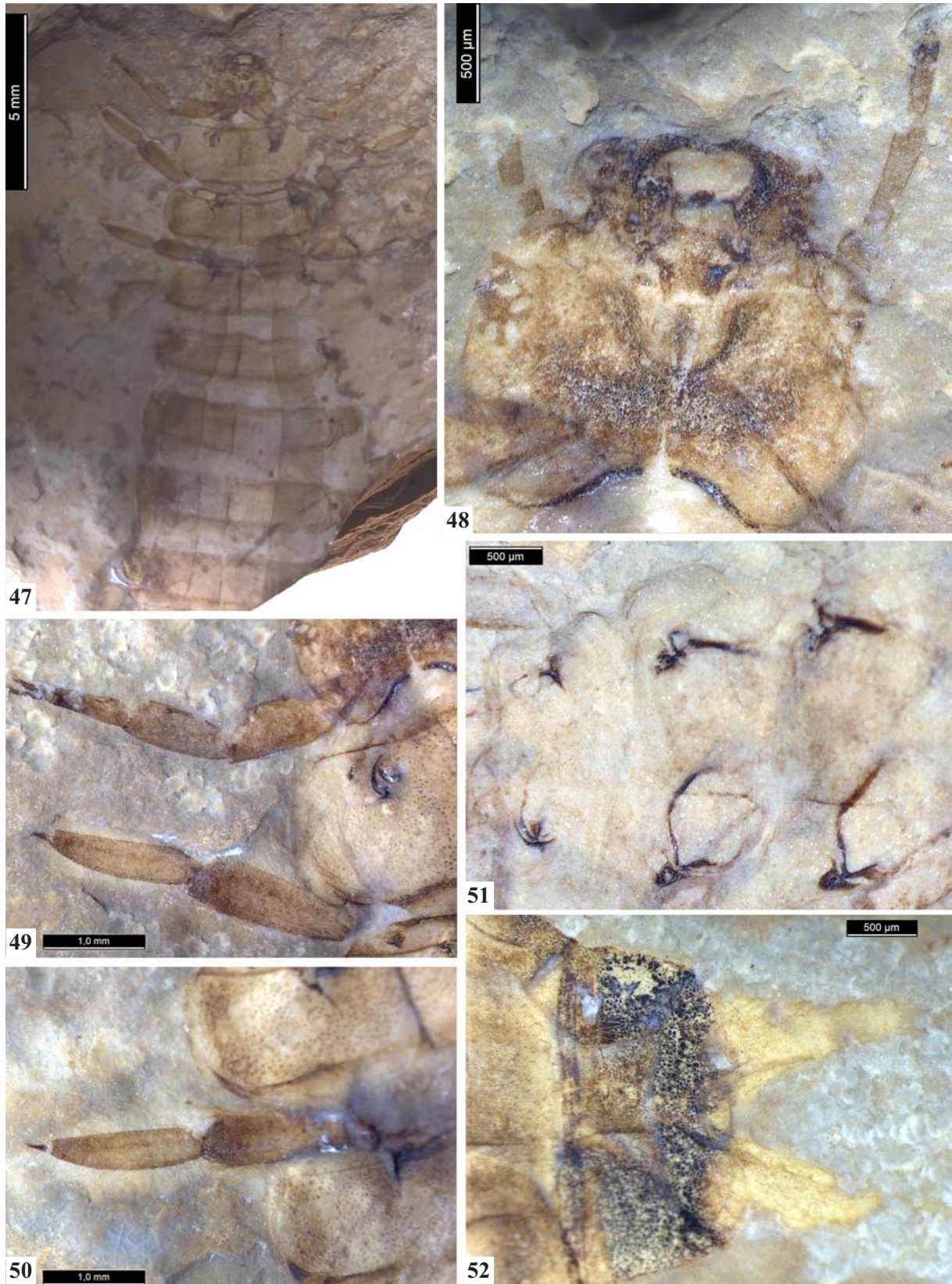
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Figs 41–43. †*Angaragabus jurassicus* Ponomarenko, 1963: 41 — general view; 42 — head; 43 — apex of abdomen; 41 — PIN1670/390; 42 — PIN509/4; 43 — PIN722/9.

Рис. 41–43. †*Angaragabus jurassicus* Пonomarenko, 1963: 41 — общий вид; 42 — голова; 43 — вершина брюшка; 41 — PIN1670/390; 42 — PIN509/4; 43 — PIN722/9.



Figs 44–46. †*Parahygrobia natans* Ponomarenko, 1977 (holotype, PIN3059/423): 44 — general view; 45 — urogomphi and body apex; 46 — head.
 Рис. 44–46. †*Parahygrobia natans* Пonomarenko, 1977 (голотип, PIN3059/423): 44 — общий вид; 45 — урогомфы и вершина брюшка; 46 — голова.



Figs 47–52. †*Stygeonectes jurassicus* Ponomarenko, 1977: 47 — general view; 48 — head; 49 — fore- and midlegs; 50 — hindlegs; 51 — thoracic apodemes; 52 — body apex; 47–51 — PIN 300/925 (holotype); 52 — PIN300/938.

Рис. 47–52. †*Stygeonectes jurassicus* Ponomarenko, 1977: 47 — общий вид; 48 — голова; 49 — средние и задние ноги; 50 — задняя нога; 51 — грудные аподемы; 52 — вершина брюшка; 47–51 — PIN 300/925 (голотип); 52 — PIN300/938.

Alarie ? Bilton, 2005; Balke et al., 2005; Beutel et al., 2006; Wang et al., 2009; Prokin et al., 2013]. In Aspidytidae [Beutel et al., 2006, fig. 13c, p. 116] it is on this segment that the folds closing the anus are positioned, confirming our interpretation.

It has to be noted that in the majority of Dytiscidae and Noteridae the tergite of segment 8 is visibly elongated and protrudes above the base of the urogomphi, and the spiracles are positioned laterally of this protrusion. This morphological feature has an obvious functional explanation: when the urogomphi of a larva that has come to the surface for breathing lie on the surface film, the spiracles are raised above the water. The closure of the spiracles in Dytiscidae [Speyer, 1922] is provided by the contraction of the same longitudinal muscles that first bring the urogomphi closer to each other and then draw them in the dorsal direction.

When a coptoclavid larva was submerged in water, the large spiracles positioned in the posterior, membranous part of tergite 8 (e.g., in †*C. longipoda*, Figs 35–38) were closed by the urogomphi, which were raised to the level of the plane of the body and drawn together. When the larva came to the surface to refill its tracheae with fresh air, the urogomphi separated, and the spiracles became open. The large, clearly discernible granulation of the urogomphi and tergite 8 in *Coptoclava* suggests that when the larva was moving quickly, these structures usually remained above the water; this is

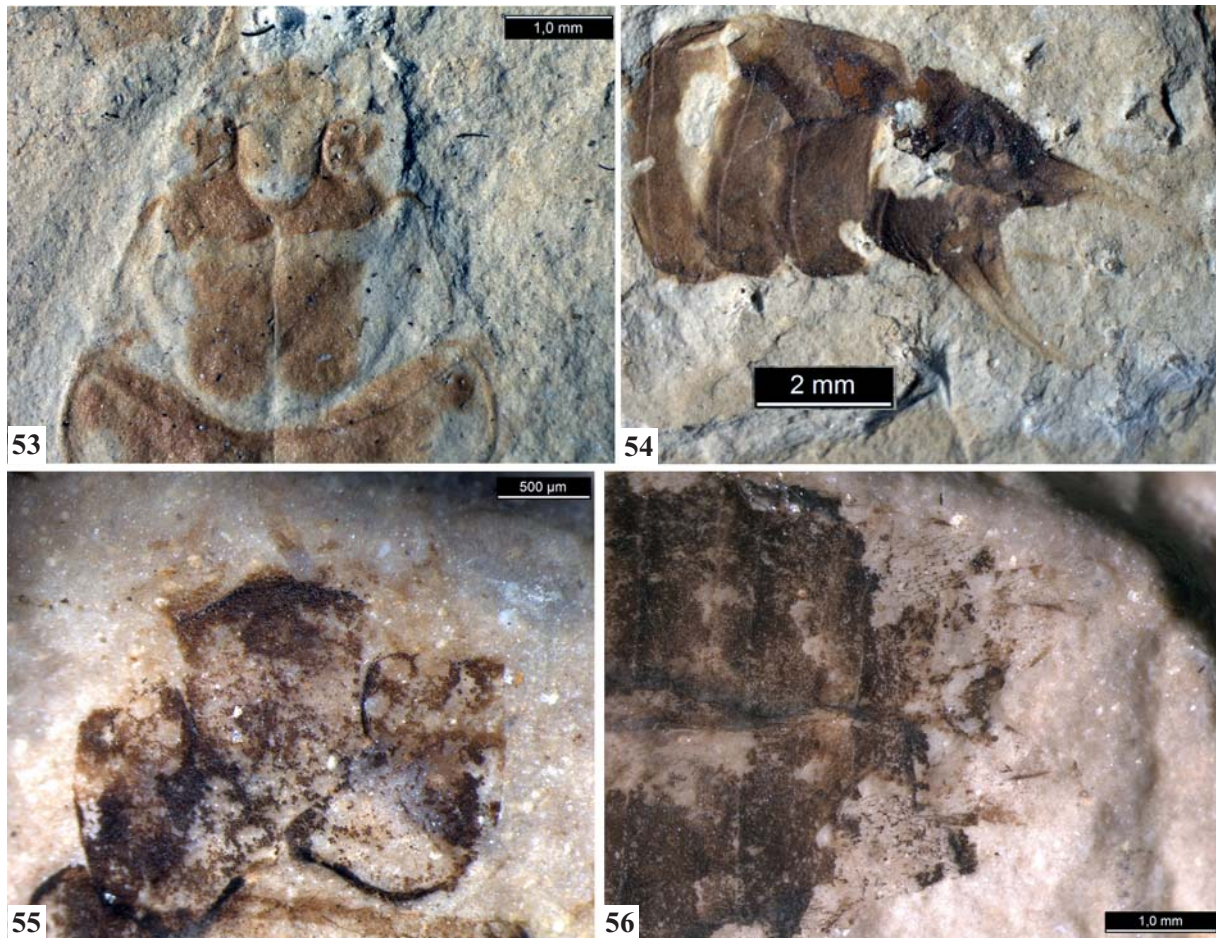
further evidence of the neustonic mode of life of the larvae of this genus.

We found a strong spiral thickening of the tracheae in †*Colymbotethis antecessor* Ponomarenko, 1993 (Figs 39–43), a member of the monotypic family †Colymbotethidae and the most archaic known representative of Dytiscoidea. Hence, this character has no important phylogenetic value for Dytiscoidea in general, since it evolved independently at least twice.

The structure of the internal margin of the mandibles of †*Protonectes germanicus* gen. et sp.n., which had three cutting surfaces without teeth, also confirms the evolutionary trend among the larvae of the family †Coptoclavidae towards a switch from “toothless” mandibles to mandibles with a strong retinaculum, but also distances †*Colymbotethis antecessor* from this trend, as does the above-discussed spiral thickening of the tracheae.

For more comprehensive comparison we have compiled the table, which represents the states of morphological characters in all described larvae of Mesozoic Dytiscoidea based on original descriptions [Ponomarenko, 1963, 1975, 1977, 1987, 1993; Ponomarenko & Martinez-Declos, 2000; Wang et al., 2009] and results of our own studies of type materials and additional materials (Figs 33–56).

The table also includes two taxa that were described as coptoclavid larvae, but currently remain inaccessible for study. †*Coptolavia africana* Teixeira, 1975 (in the text of the



Figs 53–56. †*Bolbonectes* spp.: 53–54 — †*B. occidentalis* Ponomarenko, 1993; 55–56 — †*B. intermedius* Ponomarenko, 1987; 53 — head and pronotum; 55 — head; 54, 56 — body apex; 53 — PIN3000/3222; 54 — PIN3000/3254; 55 — PIN3920/89; 56 — PIN3920/83.

Рис. 53–56. †*Bolbonectes* spp.: 53–54 — †*B. occidentalis* Ponomarenko, 1993; 55–56 — †*B. intermedius* Ponomarenko, 1987; 53 — голова и переднеспинка; 55 — голова; 54, 56 — вершина брюшка; 53 — PIN3000/3222; 54 — PIN3000/3254; 55 — PIN3920/89; 56 — PIN3920/83.

original description mentioned for a second time as “*Coptoclavia africana*”) was described from the Permian of Angola (Karoo Formation); a photograph of the impression was provided earlier [Teixeira, 1960]. †*Tuhanectes xinjiangensis* Hong, Liang et Hu, 1995 was described from the Middle Jurassic of China (Sajanfang Formation). The drawings and/or photographs of these taxa published by their authors [Teixeira, 1960; Hong et al., 1995] suggest that these taxa can indeed belong to Coptoclavidae (as well as to other aquatic or amphibiotic insects that had natatorial legs, e.g., dragonflies; †*Tuhanectes xinjiangensis* can also prove to be a member of Orthoptera).

†*Protodytiscus johillaensis* Gosh, Pal et Nandi, 2007 from the Permian-Triassic Parsora Formation (India) [Gosh et al., 2007] is not treated here, because we doubt its placement in Coleoptera.

In addition, the table includes characters of members of recent families based on our own data and published data of other authors [Alarie & Bilton, 2005; Balke et al., 2005; Beutel et al., 2006].

The numbers of characters (table), designations of character states and recent species data are taken Balke et al. [2005] for convenience of comparison (larval characters 32–53); only characters examined in fossil specimens are given;

Table. Larval character states of Mesozoic Dytiscoidea and representatives of recent Dytiscoidea families.
Таблица. Признаки личинок мезозойских Dytiscoidea и представителей рецентных семейств Dytiscoidea.

Species	Age	Character												
		32	34	39	40	49	51	53	54	55	56	57	58	59
† <i>Colymbotethis antecessor</i> Ponomarenko, 1993	T ₃	3	0	0	0	1	1	1	1*	0	0	1	0	0
† <i>Protonectes germanicus</i> gen. et sp.n.	T ₃	3	1	2	1	2	1	1	0
† <i>Daohugounectes primitivus</i> Wang, Ponomarenko et Zhang, 2009	J ₂	1	1	?1	?1	0	1	0	2	1	0	0	0	0
† <i>Stygeonectes jurassicus</i> Ponomarenko, 1977	J ₁₋₃	3	1	0	0	0	1	0	2	1	0	0	0	0
† <i>Bolbonectes intermedius</i> Ponomarenko, 1987	J ₃	2	2	0	1	0	3	1	0	0
† <i>Bolbonectes occidentalis</i> Ponomarenko, 1993	J ₃	2	2	0	1	0	3	1	0	0
† <i>Coptoclava longipoda</i> Ping, 1928	K ₁	2	2	4	0	0	1	0	3	2	0	1	0	0
?† <i>Coptolavia africana</i> Teixeira, 1975	?P or J ₃ **	1	3	0	...
?† <i>Tuhanectes xinjiangensis</i> Hong, Liang et Hu, 1995	J ₂	1	3	?1	0	...
† <i>Megacoptoclava longiurogompha</i> Ponomarenko et Martinez-Delclos, 2000	K ₁	2	...	0	0	?1	1	0	4	0	0	0	0	2
† <i>Parahygrobia natans</i> Ponomarenko, 1977	J ₃	2	0	0	0	0	1	0	2	0	0	0	0	2
† <i>Angaragabus jurassicus</i> Ponomarenko, 1963	J ₁₋₂	3	0	2	3	1	1	1	0	0	0	0	1	1
<i>Agabus</i> sp.	rec.	3	0	2	3	1	1	0	0	0	0	0	1	1
<i>Aspidytes niobe</i> Ribera et al., 2002	rec.	0	2	0	1	0	3	0	1	0	1	0	0	1
<i>Noterus crassicornis</i> (O.F. Миллер, 1776)	rec.	1	0	0	1	1	1	1	1	0	0	0	1	1
<i>Meru phyllisae</i> Spangler et Steiner, 2005	rec.	1	2	3	2	1	3	1	1	0	0	0	0	0
<i>Amphizoa lecontei</i> Matthews, 1872	rec.	3	1	1	1	1	1	1	1	0	1	0	0	0
<i>Hygrobia hermanni</i> (Fabricius, 1775)	rec.	3	0	2	0	1	2	0	1	0	0	0	1	1

ABBREVIATIONS: P — Permian; T — Triassic; J — Jurassic — K — Cretaceous; rec. — recent.

СОКРАЩЕНИЯ: P — пермь; T — триас; J — юра; K — мел; rec. — современность.

NOTES: *In Wang et al. (2009) character 54 for *Colymbotethis* is erroneously listed as (0); actually, it should be (1).

In original description of Teixeira [1975] age of fossil was dated as Permian, but according to Ponomarenko & Kirejtschuk [2013] it can be upper Jurassic. *49. Abdominal segment 10 in the majority of publications for Dytiscoidea interpreted as 9, see in the text above.

character 54, which describes larval legs (in this paper only for the mid- and hind legs), and some character states known in extinct dytiscoids are added from Wang et al. [2009]; characters 55–59 are added for the first time. Data on the morphology of the larvae of Aspidytidae and Meruidae are taken from respective publications [Alarie et al., 2005; 2011]. Some of the terms have been slightly modified here, but the meaning of the character states remains unchanged.

Therefore, in the structure of legs and mandibles †*Protonectes germanicus* **gen. et sp.n.**, the earliest known copto-clavid larva, displays a remarkably low level of “constructive perfection”, probably representing the very initial stage of mastering the nektonic mode of life.

The principal direction of the evolution of copto-clavids was mastering first nektonic predation and then neustonic predation. Morphologically this direction manifested itself in the larvae in the following processes: gradual flattening of the mid- and hindlegs and development of swimming hairs on these pairs of legs, along with differentiation of forelegs, which became raptorial; strengthening of spiral thickening of tracheae as the hydrostatic apparatus; and switch from mandible with groove, via development of retinaculum, to mandibles with several large teeth.

Certain trends can also be recognized in the evolution of adult Coptoclavidae: towards specialization of forelegs as raptorial and mid- and hindlegs as natatorial and towards differentiation of two pairs of ocelli. One of the most primitive representatives of adult copto-clavids, *Timarchopsis czechanowskii* Brauer, Redtenbacher et Ganglbauer, 1889 (= *Timarchopsis aquaticus* (Ponomarenko, 1977)) was recently placed in Caraboidea (= “Geadephaga”) [Beutel et al., 2013], doubtless erroneously in our opinion. In spite of the almost total absence of specialization of different pairs of legs, the mid- and hindlegs of this species were provided with swimming hairs and had a structure of tarsi typical of Coptoclavidae and excluding the placement of this species in Caraboidea.

The larva †*Carabilarva triassica* **sp.n.** is characterized by several important characters, which allow making several assumptions about its mode of life. The relative size of the basal and distal parts of the mandible and retinaculum shifted towards the base of the mandible are typical of recent ground beetles of the tribe Harapalini (*Ophonus* Dej., 1821 and similar genera) specialized for feeding on plant seeds [Sharova & Makarov, 2012]. The proportions of the thoracic segments and structure of the legs suggest that the larva of this new species was capable of active digging. On the whole, this set of features conforms to the habitus typical of the larvae of many recent Harapalini. But the shape of the claws of †*Car-*

abilarva triassica **sp.n.** and the age of the specimen give unambiguous evidence that this similarity is purely secondary, adaptation-related.

The larva that has been considered until now the earliest known larva of Caraboidea, †*Carabilarva jurassica* Ponomarenko, 1985 (Buryatia, Novospasskoye, Lower to Middle Jurassic, Ichetuy Formation), a weakly specialized zoophagous hemicyptobiont [Sharova & Makarov, 2012], proved almost indistinguishable by the structure of the chaetome, even to fine details, from recent larvae of the supertribe Pterostichini (Carabidae s. str.). This is evidence that it belongs rather to Protorabinae Ponomarenko, 1977 than to Eodromeinae Ponomarenko, 1977 [Makarov, 1995].

Another Jurassic larva of Caraboidea, †*Carabilarva robusta* Makarov, 1995 (Kazakhstan, Mikhailovka, Upper Jurassic, Karabastau Formation), judging by the combination of the relatively long epicranial suture, rounded wide head, and tergites without lateral bead, is closer to the larvae of Trachypachidae [Arndt & Beutel, 1995] than to most larvae of Carabidae [Makarov, 1995].

The existence in the Mesozoic of caraboid larval life forms of a recent type is by itself not surprising, especially because the adult Caraboidea of this era are also known to display a rather broad spectrum of life forms, including highly specialized ones (e.g., in the Yixian Formation). What appears important is the emergence of the carpophagous life form as early as the Triassic, that is prior to the emergence of angiosperm plants, probably as a result of feeding on gymnosperm seeds.

On the whole, rather few known Mesozoic larvae of Caraboidea are similar to recent ground beetles at the tribe level not only in general habitus, but also structurally. At the same time, the numerous Mesozoic taxa of Caraboidea described from adults are represented exclusively by members of extinct subfamilies. This probably gives evidence that the larvae of Caraboidea have considerably more conserved characters than the adults.

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EXPLANATIONS OF CHARACTERS:

32. Anterior margin of clypeolabrum: (0) with nasale distinct; (1) with nasale strongly reduced, with medial indentation; (2) with nasale strongly reduced, with medial protrusion; (3) without nasale.

34. Frontal suture: (0) Y-shaped with long stem; (1) Y-shaped with short stem; (2) V- or U-shaped with extremely reduced stem.

39. Mandible: (0) with retinaculum distinct, (1) with retinaculum strongly reduced, (2) with retinaculum absent; (3) with retinaculum absent in left mandible; (4) with three teeth.

40. Mandible: (0) without groove; (1) with groove formed of two cutting protrusions; (2) with inner canal in left mandible; (3) with inner canal in both mandibles.

49. Abdominal segment 10***: (0) developed; (1) absent.

51. Spiracle of abdominal segment 8: (0) normally developed; (1) enlarged and terminal; (2) reduced; (3) small, shifted to dorsal surface of segment 8.

53. Urogomphi: (0) longer than maximum width of head capsule; (1) shorter.

54. Middle and hind legs: (0) walking, long; (1) walking, short; (2) swimming, narrow; (3) swimming, broad; (4) reptatorial.

55. Forelegs: (0) similar with middle and hind legs; (1) grasping, short; (2) grasping, long.

56. Outer margin of mandible: (0) smooth; (1) with tab.

57. Spiral thickening of tracheae: (0) not developed; (1) developed.

58. Abdominal segment 8: (0) normal; (1) with apical appendage.

59. Segmentation of urogomphi: (0) not segmented, (1) two-segmented, (2) distinctly [? secondarily] multisegmented.

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