Biologia Serbica, 2026, 48(1):121-130 DOI: 10.5281/zenodo.20649233

Original paper

Cuticular surface microstructure in Chelodesmidae and some related families (Diplopoda: Polydesmida)

Henrik ENGHOFF

Natural History Museum of Denmark, University of Copenhagen, att.: Henrik Enghoff ZM, Øster Farimagsgade 2D, DK-1353 Copenhagen K, Denmark

Accepted: 26 February 2026 / Published online: 20 September 2026

Citation: Enghoff H. 2026. Cuticular surface microstructure in Chelodesmidae and some related families (Diplopoda: Polydesmida). In: Antić D, Makarov S, guest editors. Myriapoda in a Fractured World. Proceedings of the 20th International Congress of Myriapodology (Srebrno Jezero, Serbia). Biologia Serbica. 48(1):121-130. https://doi.org/10.5281/zenodo.20649233

Summary. The cuticular surface structures of 23 species of the family Chelodesmidae, as well as 11 species of related families, were studied using a scanning electron microscope. Cytoscute shapes were found to vary, from a regular penta-/hexagonal shape to a stretched and/or branched, jigsaw puzzle-like structure. Complicated boundaries between cytoscutes may increase cuticular stability. A row of ca. 0.001 mm long denticles was often found, mostly along the posterior margin of the cytoscutes; and may add friction by backwards movement. In a few genera, the entire cytoscute is covered with similar denticles, which in some cases may help to attach a secretal protective cover. Roundish structures visible between cytoscutes may be fungal nature.

Keywords: cuticle, cytoscutes, millipede, scanning electron microscopy.

INTRODUCTION

The cuticular surface microstructure exhibits an unbelievable diversity across arthropods (e.g., Eisenbeis and Wichard 1985). Maybe most impressively intricate (and beautiful) in Collembola (Nickerl et al. 2013), but also in millipedes (Diplopoda) a great variety of cuticular surface microstructure can be found, see, e.g., Akkari and Enghoff (2011).

In millipedes (Diplopoda) and centipedes (Chilopoda), a very common cuticle pattern consists of hexa- and pentagonal scutes with a diameter between 0.005 and 0.01 mm (Fig. 1), which are believed to be secreted by individual epidermal cells (Fusco et al. 2000; Moretto et al. 2015), and have therefore been labeled 'cytoscutes' („cell-shields") by, e.g., Hannibal and May (2021) and Enghoff et al. (2025). Cytoscutes of various shapes and structures are known from many other arthropods, such as Symphyla (Eisenbeis and Wichard 1985: plate 79f), and Diptera (Rebora et al. 2023).

Chelodesmidae represents a large family of flat-backed millipedes (order Polydesmida), with approximately 800 described species distributed in the Neotropics, Afrotropics and – marginally – the southwestern part of the Palaearctic. Although most species are forest-dwellers, some species have been found in caves (Mauriès and Geoffroy 2000; Bouzan et al. 2022). Morphologically, the family is very diverse, showing a wide range of gonopod configurations, body sizes (between 2-3 cm and 10 cm in body length, Pena-Barbosa et al. 2013), surface sculptures, paranotal shapes and coloration. Some species clearly display aposematic coloration, e.g., *Eucampesmella macunaima* Bouzan, Iniesta, Pena-Barbosa and Brescovit, 2021, *Chondrodesmus riparius* Carl, 1914, *Morogorius divisus* Enghoff, 2025 (Bouzan et al. 2021: figs 2–4; Golovatch et al.

E-mail: henghoff@snm.ku.dk

2025: fig. 4; Enghoff et al. 2025: fig. 2), suggesting a relatively non-cryptic lifestyle among these species.

As part of a study of East African species of the family (Enghoff et al. 2025), the shape of the cytoscutes was found to be highly variable between species. This prompted a broader study of several African and Neotropical genera of Chelodesmidae, as well as a few representatives of related families. The present study was conducted to investigate shape variation as a potential source of phylogenetic information, as well as the possible functional significance of different cytoscute shapes and associated structures, such as „denticles" and „intercalary microscutes" (see below).

MATERIAL AND METHODS

Midbody body rings, or partial midbody rings, were isolated from individuals available in the collection of the Natural History Museum of Denmark (NHMD). In total, 37 specimens representing 34 species: corresponding to one individual from each species, and four from *Tanzaniella howelli* Hoffman, 1977. Identifications were mainly conducted by the late R.L. Hoffman or the author. Specimens were cleaned by ultrasound, transferred from 70% to 96% ethanol and then to acetone, air-dried, mounted on aluminum stubs, and coated with a 12 nm layer of platinum-palladium using a Quorum SC7620 Mini Sputter Coater. The dorsal side of the paranota was examined using a Zeiss Gemini 360VP scanning electron microscope (SEM) in NHMD. For a few species, a persistent cover of some secretion made observation of the cuticular surface impossible, despite treatment with ultrasound, laundry enzyme and/or sodium hypochlorite (NaOCl). Images were processed to adjust contrast and brightness in Adobe Photoshop, which in some cases involved stacking multiple images. Plates were composed using Microsoft Publisher. The results are summarized in Table 1, and examples of the cytoscutes are shown in Figs 1–4.

RESULTS

A basic pattern of hexagonal and pentagonal cytoscutes was observed for several genera belonging to Chelodesmidae, Xystodesmidae, Oxydesmidae, Gomphodesmidae, Sphaeriodesmidae and Paradoxosomatidae (Fig. 1). In many cases, the cytoscutes were found to be located strictly in one plane, in a pavement-like arrangement (Fig. 1A–C), while for others they displayed a tendency for imbrication (Fig. 1D). In many species, a row of tiny (0.001 mm or less) denticles was seen along one margin (mainly the posterior margin) of some or all cytoscutes (Figs 1B, 2D, 4A). Another frequent feature was the presence of rows of circular, slightly to moderately protruding structures, referred to as intercalary microscutes (Akkari and Enghoff 2011; Shear et al. 2016) (Figs 1C, D, 2A, B, 4D). The images shown in Figs 1–4 all show the structure on the dorsal side of a midbody paranotum, and in order to check for constancy, twelve images were made from various parts of the left paranotum of a male *Tanzaniella howelli*. All images showed the same very stretched, branched shape, but the possible occurrence of the same shape on other body parts was not investigated. For most species, only a single specimen was studied; however, for *Tanzaniella howelli*, all of the four investigated specimens, including a juvenile, were found to have similar cytoscutes.

Modifications of the basic pattern were observed, consisting of changes in shape, and/or changes in surface structure.

Cytoscutes are very often roughly isodiametric in shape, but they may also be more or less elongated (Fig. 2G), and their margins may be differently curved or undulated (Fig. 2E, F). Elongation and margin curving/undulation may combine to form rather intricate, sometimes branched shapes (Fig. 3), including the very slender (~5 times longer than broad), ghostlike cytoscutes observed in *Tanzaniella howelli* (Fig. 3F) and the „jigsaw puzzle pieces" seen in *Chondrodesmus riparius* Carl, 1914 (Fig. 3B). In *Henrisaussurea corcovadis* (Brölemann, 1903) (Fig. 4A), the cytoscutes are moderately elongated and branched, and in addition the tiny marginal denticles are much longer than normal (~0.002 mm, *vs* ~0.001 mm); although they remain confined to one side of the cytoscute.

In contrast, results observed in the species from the genus *Callistocilla* Hoffman, 1977 were very different. Here the cytoscutes are of a very regular hexa-/pentagonal shape, while the entire surface, not only one margin, is covered with minute denticles, somewhat reminiscent of a fakir 'bed-of-nails' (Fig. 4B). A similar modification may also occur in *Cryptoporatia* sp. (Fig. 4C), in this species the cuticle was covered by a layer of secretion which proved extremely difficult to remove. Neither ultrasound, mechanical scratching nor treatment with commercial laundry enzyme could remove this secretion layer. Nor could a short dip in sodium hypochlorite. Eventually a piece of paranotum was left in NaOCl overnight at room temperature. This removed the secretion but also destroyed the cuticle. Still, hexagonal/pentagonal cytoscutes are visible (Fig. 4C), as well as the usual row of marginal denticles. In addition, a number of small holes were seen scattered over the surface of many cytoscutes; which may be remnants of denticles similar to those seen in *Callistocilla*.

Finally, a unique surface structure consisting of irregular dimples and vaguely reminiscent of the surface of certain types of biscuits was seen in the aphelidesmid *Haematotropis divergens* (Chamberlin, 1918) (Fig. 4D).

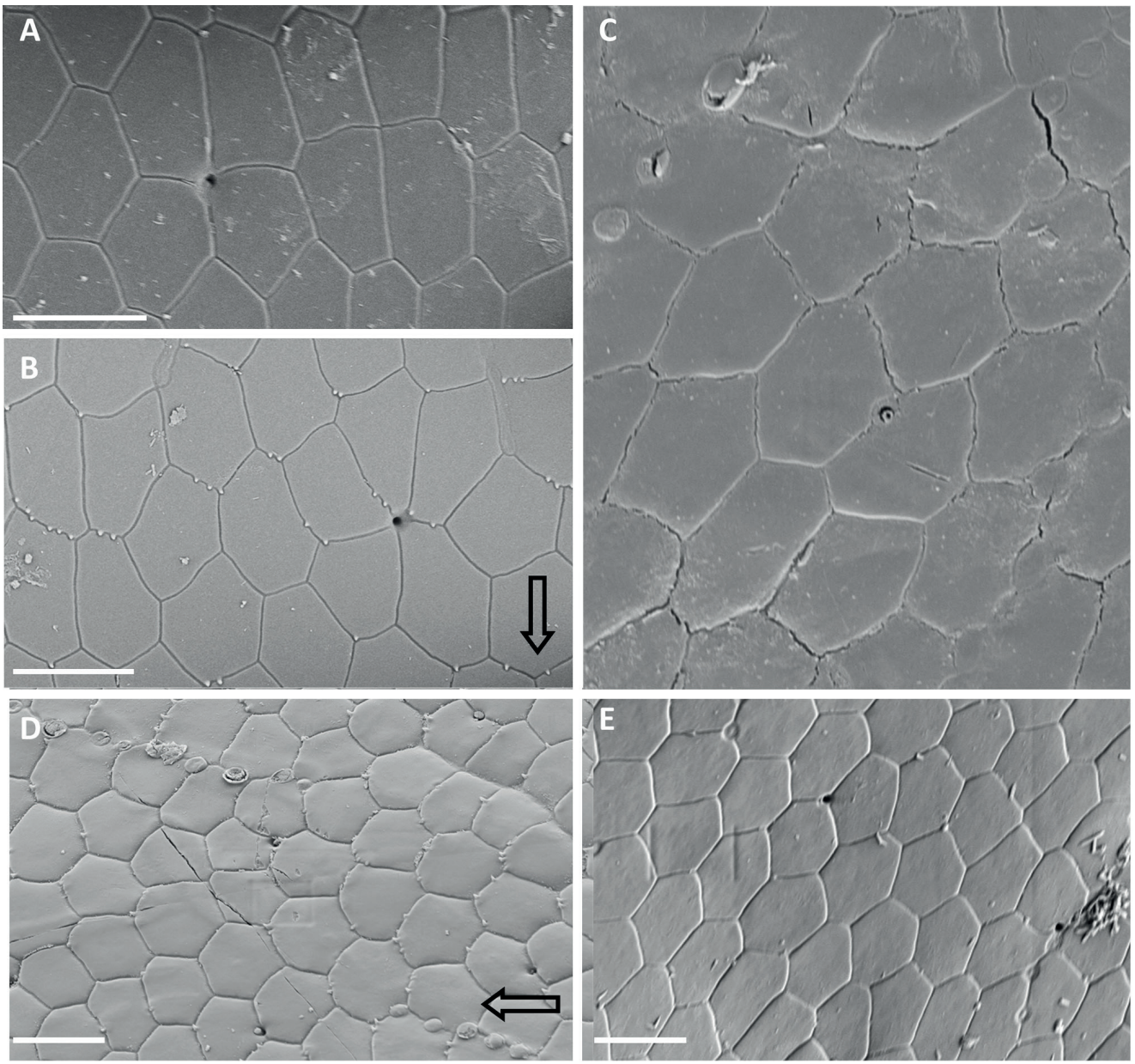

Fig. 1. Dorsal microsculpture of midbody paranota. **A**-**B**, *Oxidus gracilis* (C.L. Koch, 1847) (no collection number, Paradoxosomatidae); **B** showing tiny denticles along the posterior margin of the cytoscutes. The arrow points backward; **C**, *Strongylomorpha bohlsi* (Attems, 1898) (NHMD 1184581, Chelodesmidae); **D**, *Kilimagomphus massaiensis* (Attems, 1938) (NHMD 118761, Gomphodesmidae), showing rows of enigmatic (fungal?) structures between cytoscutes and tiny denticles along the posterior margin of the cytoscutes. The arrow points backward; **E**, *Melaphe vestita* (C.L. Koch, 1847) (NHMD 1184747, Xystodesmidae). (Scale bars: = 0.01 mm.)

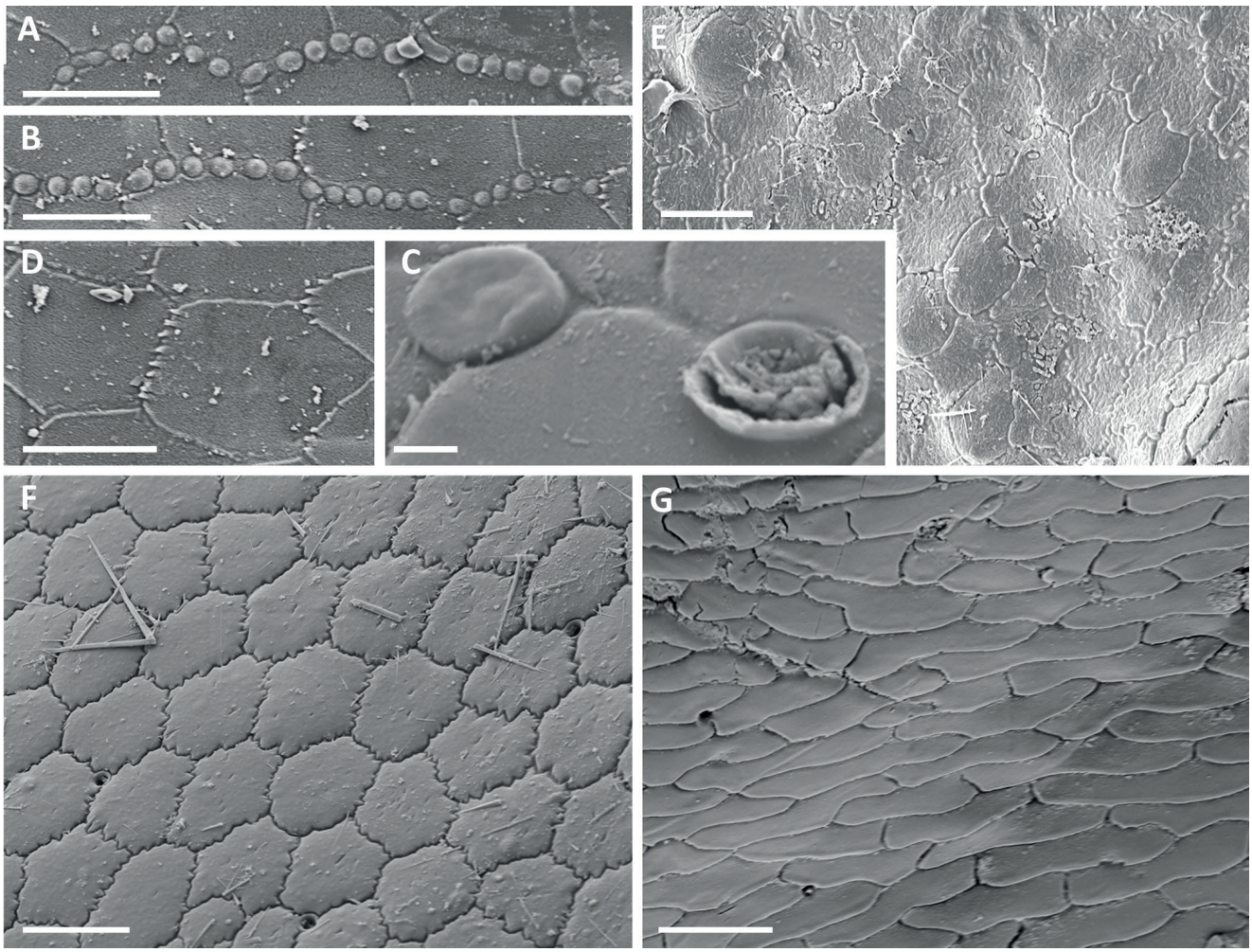

Fig. 2. Dorsal microsculpture of midbody paranota. **A**, **B**, **D**, *Trichomorpha nidicola* Chamberlin, 1925 (NHMD 1184760, Chelodesmidae); **A**, **B**, fungal? structures between cytoscutes; **D**, denticles along the posterior margin of the cytoscute; **C**, *Kilimagomphus massaiensis* (Attems, 1938) (NHMD 118761, Gomphodesmidae), fungal? structures between cytoscutes; **E**, *Cheirodesmus discolor* Cook, 1896 (NHMD 1184582, Chelodesmidae); **F**, *Sigmoria nigrimontis* (Chamberlin, 1947) (NHMD 1184748, Xystodesmidae); **G**, *Eurydesmus zebratus* (Gervais, 1836) (NHMD 1184589, Chelodesmidae). (Scale bars: A, B, D–G = 0.01 mm; C = 0.001 mm.)

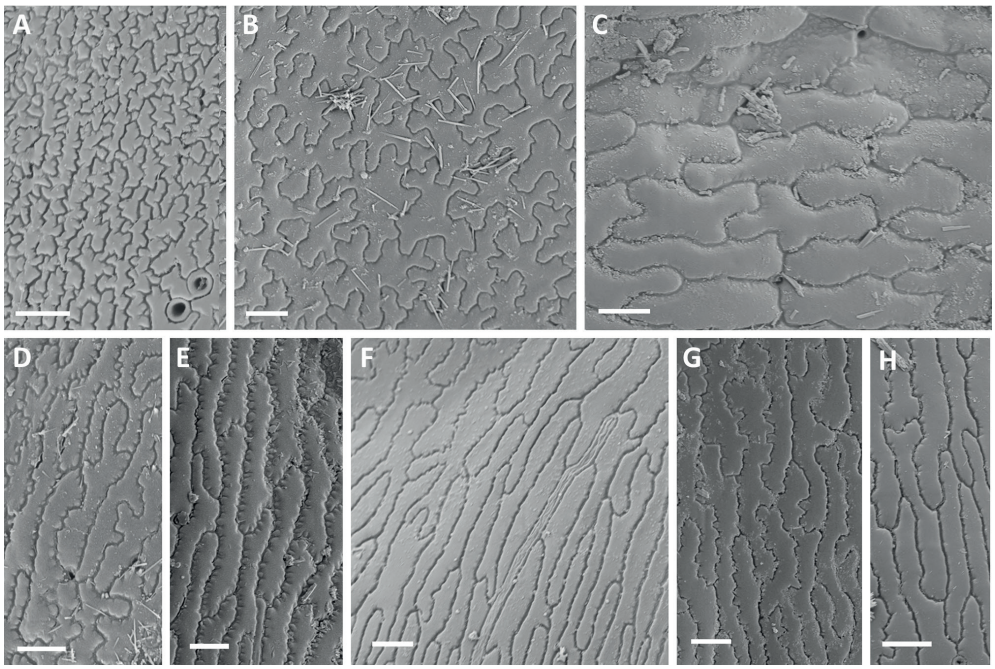

Fig. 3. Dorsal microsculpture of midbody paranota. **A**, *Paracordyloporus* aff. *camerunensis* Attems, 1927 (NHMD 1184753, Chelodesmidae); **B**, *Chondrodesmus riparius* Carl, 1914 (NHMD 1184588, Chelodesmidae); **C**, *Afolabina yoruba* Hoffman, 1967 (NHMD 1184751, Chelodesmidae); **D**, *Tylodesmus amoebus* Cook, 1896 (NHMD 1184750, Chelodesmidae); **E**, *Prepodesmus tigrinus* Cook, 1896 (NHMD 1184566, Chelodesmidae); **F**, *Tanzaniella howelli* Hoffman, 1977 (NHMD 118466, Chelodesmidae); **G**, *Morogorius kitungulu* Enghoff, 2025 (NHMD 1184573, Chelodesmidae); **H**, *Dionaeadesmus force* Enghoff, 2025 (NHMD 1184572, Chelodesmidae). (Scale bars: = 0.005 mm.)

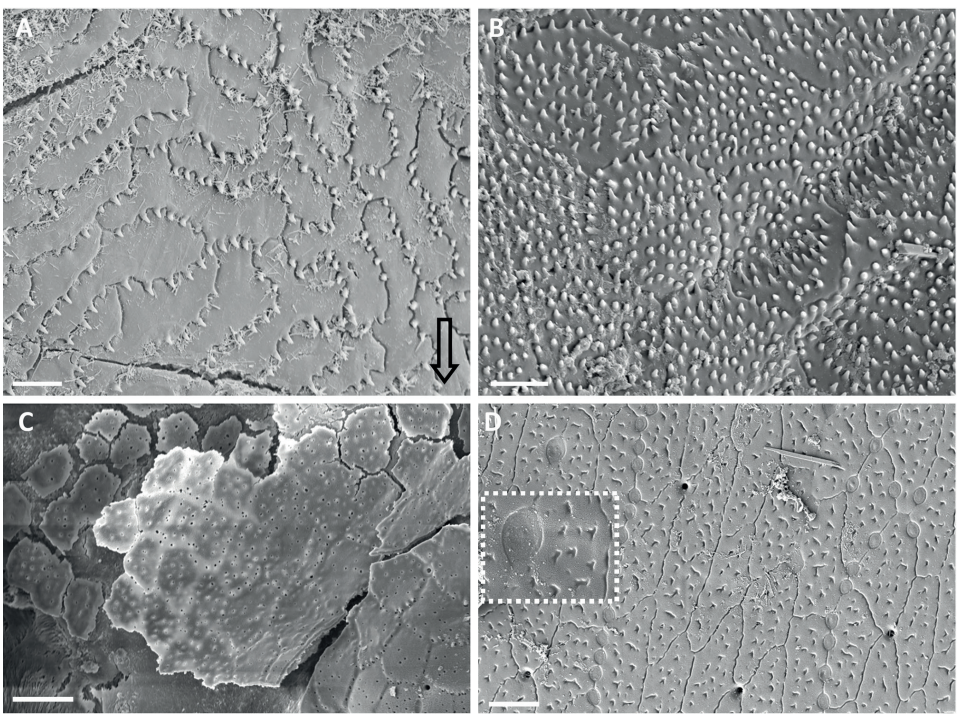

Fig. 4. Dorsal microsculpture of midbody paranota. **A**, *Henrisaussurea corcovadis* (Brölemann, 1903) (NHMD 1184580, Chelodesmidae), showing enlarged denticles mostly along the posterior margin of the cytoscutes; **B**, *Callistocilla dolorotrix* Hoffman, 2005 (NHMD 1184742, Chelodesmidae); **C**, *Cryptoporatia* Hoffman, 1980 sp. (NHMD 1184752, Chelodesmidae) after overnight treatment with NaOCl; **D**, *Haematotropis divergens* (Chamberlin, 1918) (NHMD 1184590, Aphelidesmidae) – inset: close-up of peculiar surface and inter-scute microstructure. (Scale bars: A, B, D = 0.005 mm; C = 0.01 mm.)

Table 1. Studied specimens and brief characterization of cuticular surface structure.

Family	Species	Collecting data	Surface pattern
CHELODESMIDAE	*Afolabina yoruba* Hoffman, 1967	**GHANA** • ♂; Legon, Botanical Garden; 11 May 1965; V. Schiøtz leg. NHMD 1184751	Fig. 3C: Cytoscutes moderately stretched, "amoeba-like".
CHELODESMIDAE	*Alocodesmus hanseni* Silvestri, 1898	**VENEZUELA** • ♂; before 1897; Levinsen leg.; NHMD 1184746	Typical diplopod pattern: Hexa-/pentagonal cytoscutes.
CHELODESMIDAE	*Anisodesmus sceptrifer* (Demange & Mauriès, 1975)	**GUINEA** • ♂; N'Zérékoré 13–15 May 1950; Galathea-Exp. Leg.; NHMD 1184749	As *Tylodesmus amoebus* (Fig. 3D)
CHELODESMIDAE	*Callistocilla dolorotrix* Hoffman, 2005	**TANZANIA** • ♂; Iringa Region, Kilolo District, Udzungwa Scarp Nature Reserve, Chita Juu; 8°32′23.4″ S, 35°51′36.0″ E; 1387 m a.s.l.; 1 Feb. 2022; A. Ngute, R. Malanda, W. Mhagawale, H. Mnendendo, A. Mpoto and A. Marshall leg.; FoRCE Plot 109, open canopy, COLL.NHMD - ACC. NO. 2022-EN-003; NHMD 1184742	Fig. 4B: Cytoscutes regularly hexa-/pentagonal, with dense cover of microdenticles, not only along one margin.
CHELODESMIDAE	*Callistocilla beatrix* Hoffman, 1977	**KENYA** • ♂ holotype; Tiwi S of Mombasa; 18 May 1968; Schiøtz leg.; ZMUC 00101515.	as *C. dolorotrix* (Fig. 4B).
CHELODESMIDAE	*Callistocilla* ?n. sp.	**TANZANIA** • ♂; Morogoro Region, Kanga Mts, Kanga Forest Reserve; 400–500 m a.s.l.; 22–25 Nov. 1984; N. Scharff leg.; lowland rain forest; NHMD 1184571.	as *C. dolorotrix* (Fig. 4B).
CHELODESMIDAE	*Cheirodesmus discolor* Cook, 1896	**SIERRA LEONE** • ♂; Joru; 1 Jul. 1963: V. Schiøtz leg.; NHMD 1184582	Fig. 2E: Cytoscutes roughly isodiametric, with somewhat irregular, partly curved edges.
CHELODESMIDAE	*Chondrodesmus riparius* Carl, 1914	**DENMARK** • ♂; Copenhagen, Østerbro, indoor in potted palm (*Phoenix roebelini* O'Brien); Jan.–Mar. 2007; A. Thomsen & H. Enghoff leg. NHMD 1184588	Fig. 3B: Cytoscutes roughly isodiametric, with strongly irregular edges, very much like jigsaw puzzle pieces.
CHELODESMIDAE	*Cryptoporatia* sp.	**NIGERIA** • ♂; E, Osomba 56 miles from of Calabar; 17 Jun. 1965; V. Schiøtz leg.; NHMD 1184752	Fig. 4C: Cytoscutes after brutal removal of a secretion layer covering, regularly hexa-/pentagonal, with dense cover of pores which may represent dissolved microdenticles.
CHELODESMIDAE	*Diaphorodesmus dorsicornis* (Porat, 1894)	**NIGERIA** • ♂; Cross Rivers State, Osomba 56 miles N of Calabar; 17 Jun. 1965; V. Schiøtz leg.; NHMD 1184759	Cytoscutes hexa-/pentagonal, slightly stretched.
CHELODESMIDAE	*Dionaeadesmus force* Enghoff, 2025	**TANZANIA** • ♂ paratype; Iringa Region, Mahenge District, West Kilombero Scarp Forest Reserve, Nyumbanitu Mts, S Udekwa Village; 07°48′ S, 36°21′ E; 2300 m a.s.l.; Dec. 1993; L.L. Sørensen & J.O. Svendsen leg.; NHMD 1184572.	Fig. 3H: Cytoscutes stretched, slightly branched.
CHELODESMIDAE	*Eurydesmus zebratus* (Gervais, 1836)	**BRAZIL** • ♂; Rio de Janeiro; 1850–1856; J. T. Reinhardt leg.; NHMD 1184589	Fig. 2G: Cytoscutes stretched.
CHELODESMIDAE	*Henrisaussurea corcovadis* (Brölemann, 1903)	**BRAZIL** • ♂; Faz. Do Cachoeira; before 1894; Böving-Petersen leg.; NHMD 1184580	Fig. 4A: Cytoscutes stretched, partly branched, microdenticles in marginal row stronger than usual.
CHELODESMIDAE	*Iguazus ?ornithopus* (Brölemann, 1902)	**BRAZIL** • ♂; Lagoa Santa; 1850–1856; J. T. Reinhardt leg.; NHMD 1184583	as *Eurydesmus zebratus* (Fig. 2G).
CHELODESMIDAE	*Morogorius kitungulu* Enghoff, 2025	**TANZANIA** • ♂ holotype; Udzungwa Mts, Kitungulu Forest Reserve; 08°09′ S, 36°05′ E; 1500 m a.s.l.; Jan. 1996; M. Andersen, P. Gravlund and A. Jakobsen leg.; NHMD 1184573.	Fig. 3G: Cytoscutes stretched, with strongly irregular edges.

CHELODESMIDAE	*Morogorius divisus* Enghoff, 2025	**TANZANIA** • ♂ paratype; Iringa Region, Kilolo District, Udzungwa Scarp Nature Reserve, Uhafiwa; 8°31′58.404″ S, 35°51′28.368″ E; 1375 m a.s.l.; 25 Jan. 2022. A. Ngute, R. Malanda, W. Mhagawale, H. Mnendendo, A. Mpoto and A. Marshall leg.; FoRCE Plot 106, open canopy; COLL.NHMD - ACC. NO. 2022-EN-003; NHMD 1184702	as *M. kitungulu* (Fig. 3G).
CHELODESMIDAE	*Morogorius louishanseni* Enghoff, 2025	**TANZANIA** • ♂ paratype; Iringa Region, Mahenge Distr., West Kilombero Scarp Forest Reserve, Nyumbanitu Mts, S Udekwa Village; 07°48′ S, 36°21′ E; 1500 m a.s.l.; Dec. 1993; J.O. Svendsen leg.; NHMD1184713	as *M. kitungulu* (Fig. 3G).
CHELODESMIDAE	*Paracordyloporus* aff. *camerunensis* Attems, 1927	**NIGERIA** • ♂; Eastern State, 56 miles north of Calabar; 17 Jun. 1965; V. Schiøtz leg.; NHMD 1184753	Fig. 3A: Cytoscutes stretched, with strongly irregular edges.
CHELODESMIDAE	*Prepodesmus tigrinus* Cook, 1896	**GHANA** • ♂; Bimpang Forest Reserve 45 miles NNW of Cape Coast; 6 May 1963; D. Barry leg.; NHMD 1184566	Fig.3E: Cytoscutes stretched, with finely undulate edges.
CHELODESMIDAE	*Strongylomorpha bohlsi* (Attems, 1898)	**PARAGUAY** • ♂; Asuncion – San Lorenzo; 26 Sep. 1988; Bretzendorfer leg.; NHMD 1184581	Fig. 1C: Typical diplopod pattern: Hexa-/pentagonal cytoscutes, often with row of microdenticles along one side.
CHELODESMIDAE	*Tanzaniella howelli* Hoffman, 1977	**TANZANIA** • ♂; Morogoro Region, Kilombero District, Udzungwa Mountains National Park, Mwanihana; Sanje; 7°46′52.14″ S, 36°54′11.7714″ E; 421 m a.s.l.; 20 Feb. 2022; A. Ngute, E. Kivambe, R. Malanda, W. Mhagawale, H. Mnendendo and A. Marshall leg.; open canopy. ForCE Plot 92: COLL.NHMD - ACC. NO. 2022-EN-003; NHMD 1184661	Fig. 3F: Cytoscutes strongly stretched, slightly branched.
CHELODESMIDAE	*Trichomorpha nidicola* Chamberlin, 1925	**PANAMA** • ♂; Prov. Panama, Gamboa (TT or PR); 1983–1984; W. Nentwig leg.; NHMD 1184760	Typical diplopod pattern: Hexa-/pentagonal cytoscutes.
CHELODESMIDAE	*Tylodesmus amoebus* Cook, 1896	**LIBERIA** • ♂; Bomi Hills; 9 Aug. 1949; S. Herold Olsen leg.; NHMD 1184750	Fig. 3D: Cytoscutes stretched, with strongly irregular edges.
APHELIDESMIDAE	*Haematotropis divergens* (Chamberlin, 1918)	**TRINIDAD AND TOBAGO** • ♂; Trinidad, Simla, 300 m a.s.l.; 10 Feb. 1983; J. Nielsen leg.; rain forest; NHMD 1184590	Fig. 4D: Cytoscutes stretched, with "biscuit surface-like" structure.
GOMPHODESMIDAE	*Agrophogonus hamulifer* Olsen & Enghoff, 2020	**TANZANIA** • ♂; Morogoro Region, Kilombero District; Magombera Nature Reserve, 7°48'55.548" S, 36°58'37.812" E; 281 m a.s.l.; 28 Dec. 2019; A. Ngute & A.M. Marshall leg.; micro-FoRCE plot 8, open forest NHMD 1184757	Typical diplopod pattern: Hexa-/pentagonal cytoscutes.
GOMPHODESMIDAE	*Gomphodesmus castaneus* Cook, 1896	**TANZANIA** • ♂; Amani, Forest House; ca. 1000 m a.s.l.; 2 Aug. 1974; I.B. & H. Enghoff leg.; in litter; ZMUC 2000226	Typical diplopod pattern: Hexa-/pentagonal cytoscutes.
GOMPHODESMIDAE	*Kilimagomphus massaiensis* (Attems, 1938)	**TANZANIA** • ♂; Kilimanjaro; 3°15'27.36" S, 37°25'1.5594" E; 19 Jun. 2012; J. Röder leg.; lower montane forest; NHMD 118761	Fig. 1D: Typical diplopod pattern: Hexa-/pentagonal cytoscutes, often with row of microdenticles along one side.
OXYDESMIDAE	*Gonepacra lescurei* (Demange, 1977)	**TANZANIA** • ♂; Morogoro Region, Morogoro District Uluguru Mts., Mkungwe Forest Reserve; 6°51–6°54 S, 37°51–37°56 E; 400–1000 m a.s.l.; Aug. 2000; N. Doggart leg.; submontane forest, Uluguru Mountains Biodiversity Conservation Project; NHMD 1184758	Cytoscutes regularly hexa-/pentagonal.

PARADOXOSOMATIDAE	*Oxidus gracilis* (C.L. Koch, 1847)	**DENMARK** • ♀; NEZ, Roskilde, Plantecenter "Hobbyland"; 8 Feb, 2025, L. H. Hansen; not registered	Fig. 1A, B: Typical diplopod pattern: Hexa-/pentagonal cytoscutes, often with row of microdenticles along one side.
SPHAERIODESMIDAE	*Sphaeriodesmus filamentosus* Loomis, 1974	**PANAMA** • ♂; Gamboa Pipeline Road; 30 Jul. 1983; N. Scharff leg.; rain forest; NHMD 1184592	Typical diplopod pattern: Hexa-/pentagonal cytoscutes.
XYSTODESMIDAE	*Gyalostethus monticolens* (Chamberlin, 1951)	**USA** • ♂; Tennessee, Cocke Co., Great Smoky Mts National Park, Cosby area; 8 Aug. 1981; H. Enghoff & R.M. Shelley leg.; NHMD 1184755	Like *Sigmoria nigrimontis* (Fig. 2F), but edges a bit less undulating.
XYSTODESMIDAE	*Levizonus thaumasius* Attems, 1898	**RUSSIA** • ♂; Maritime Province, haika Station 14th km, just near Vladivostok; 9 May 1977; E.V. Mikhaljove leg.; oak wood litter; NHMD 1184578	Typical diplopod pattern: Hexa-/pentagonal cytoscutes.
XYSTODESMIDAE	*Melaphe vestita* (C.L. Koch, 1847)	**TURKEY** • ♂; Edirne Province, Kuxu Dağ SE Keşan; 350 m a.s.l.; 9 May 1995; H. Enghoff, M. Frater & H. Read leg.; *Pinus/Quercus* forest; NHMD 1184747	Fig. 1E: Typical diplopod pattern: Hexa-/pentagonal cytoscutes, often with row of microdenticles along one side.
XYSTODESMIDAE	*Sigmoria nigrimontis* (Chamberlin, 1947)	**USA** • ♂; North Carolina, McDowell Co., 9.6 miles NW Marion, along US Forest Service Road; 25 Jul. 1975; A.M. Shelley & J.C. Clamp leg; NHMD 1184748	Fig. 2F: Cytoscutes of normal shape but with undulating edges.

DISCUSSION

When comparing the relatively striking variations in cytoscute shape documented above, it should be noted that cytoscute structures exhibit considerable variation between different body parts of the same specimen. A single piece of evidence, viz., SEM images from a paranotum of a specimen of *Tanzaniella howelli* suggests, however, that cytoscute shape remains fairly constant over the entire paranotum.

The pattern of hexa-/pentagonal cytoscutes has previously been reported for many groups of millipedes, including Cambalidae (Reboleira et al. 2015: fig. 3D), Odontopygidae (Enghoff 2014: fig. 34), Spirostreptidae (Enghoff 2017: fig. 18C), Dorypetalidae (Reboleira and Enghoff 2015: fig. 3C), Blaniulidae (H. Enghoff, unpubl. observations on several species), Siphoniulida (Recuero et al. 2026), as well as in centipedes (e.g., Fusco et al. 2000; Moretto et al. 2015; Stoev et al. 2015; Edgecombe and Giribet 2016).

The row of ~0.001 mm denticles found in several species (Figs 1B, D, 2D, 4A) is intriguing. These denticles predominantly occur on the posterior margin of each cytoscute and point backwards (Fig. 1B, D). Often, they are seen only on some cytoscutes, and it cannot be excluded that they exist on some cytoscutes in species where they have not been detected. Their position suggests that they may increase friction by backwards movement (Thies Büscher, pers. comm.). Even in *Henrisassurea corcovadis* (Fig. 4A) in which cytoscute shape is quite irregular, the denticles – which are particularly long in this species – predominantly occur along the posterior margin of the cytoscutes. Similar denticles also occur along the posterior margin of cytoscutes in Odontopygidae (Frederiksen and Enghoff 2015: fig. 3D; Enghoff 2018: fig. 4) in Julidae (Eisenbeis and Wichard 1985: plate 63) and Symphyla (Eisenbeis and Wichard 1985: plate 79). In some species of the orders Polyzoniida and Siphonophoridae, rows of similar denticles also exist even though the cuticular surface does not display a cytoscute structure (Moritz et al. 2022: fig. 9b; Anilkumar et al. 2022: fig. 4d; Marek et al. 2016: fig 4a; Moritz and Parra-Gomez 2023: figs 4g, 5).

Intercalary microscutes (Figs 1D, 2A–C, 4D) are also known from other millipede groups, including several other families of Polydesmida (Akkari and Enghoff 2011; Shear et al. 2016), as well as Odontopygidae (Enghoff 2014), Cambalidae (Reboleira et al. 2015), and Dorypetalidae (Reboleira and Enghoff 2015). They are regularly circular in shape, and may be more or less protruding, in some cases even stalked (Enghoff and Reboleira 2017: fig. 4D), and may be connected by narrow strips between the regular cytoscutes. Enghoff and Reboleira (2017) suggested that they may be fungal nature, and they do indeed show resemblance to conidia of the entomopathogenic fungus *Beauveria bassiana* (Bals.-Criv.) Vuill. (Güerri-Agulló et al. 2010: fig. 7). The similarity to *B. bassiana* is particularly striking for the structures found on the odontopygid millipede *Chaleponcus nikolajscharffi* Enghoff, 2014 by Enghoff and Reboleira (2017: fig. 4C, D).

The paranota, also called keels, of polydesmidan millipedes serve as „wedges" during burrowing, especially through layers of leaf litter (Manton 1977: 356). The two main types of modifications to cytoscute shape have different

implications in terms of possible function.

Elongation, and in particular branching of the cytoscutes probably serves to increase mechanical stability. The very branched, jigsaw puzzle piece-like cytoscutes seen, for example in *Chondrodesmus riparius* (Fig. 3B) very much remind one of certain plant epidermal cells: see, e.g., Muntoreanu et al. (2011: fig. 3). Liu et al. (2021) analyzed the formation of jigsaw puzzle piece-like plant epidermis cells. They concluded (p. 544) that „Extensive phylogenetic analyses of pavement cell shape across plant species suggest that no single function has driven the evolution of the puzzle shape, and therefore many proposed functions for this shape may hold true for certain species and growth conditions." and that „The various functions for pavement cell interdigitation that have been proposed include cell spacing and enhancement of tissue integrity, mechanical strength and flexibility, as well as growth plasticity and resistance to turgor pressure–induced mechanical stresses on the cell walls." For the most part, these observations could equally apply to millipede cytoscutes, although the shape of the epidermal cells will not necessarily match that of the overlying cytoscutes (see, e.g., Büscher et al. 2018). In any case, the hard cuticle may functionally replace solid cell walls which are present in plants, but absent in millipedes.

The dense cover of microdenticles on the cytoscute surface seen in *Callistocilla* (Fig. 4B) and possibly in *Cryptoporatia* Hoffman, 1980 (Fig. 4C), as well as the enlarged marginal denticles seen in *Henrisassurea* Hoffman, 1971 (Fig. 4a), could potentially help to fix a protective cover composed of secretions. Cuticular microsculpture or a dense cover of tiny hairs has been seen in several other millipedes which are covered by a secretion and/or an incrustation of soil particles, e.g., species of *Cryptocorypha* Attems, 1907 and *Elythesmus enghoffi* (Hoffman, 1978) (Enghoff 2022), and several species of Pyrgodesmidae (Shear 1977). In *Cryptoporatia* a secretion cover was found to be present that is almost impossible to remove, but in *Callistocilla* and *Henrisaussurea* there is no layer of secretion on the cuticle. The function of the microdenticles in this case could be to increase friction, non-directionally in the case of *Callistocilla*.

The cuticular surface microstructure potentially could bear phylogenetic signals, which might contribute to resolve the phylogeny of Chelodesmidae – a very poorly understood family. The material studied here provides a few more or less vague such signals:

- In the East African genera *Morogorius* Verhoeff, 1941, *Tanzaniella* Hoffman, 1977 and *Dionaeadesmus* Enghoff, 2025 the cytoscutes are elongated, very narrow and more or less branched (Enghoff et al. 2025). Some other African genera (*Prepodesmus* Cook, 1896, *Tylodesmus Cook, 1895*) have more or less similar cytoscutes, but so far, this cytoscute shape has not been seen in any Neotropical genus.
- In all three species of *Callistocilla* studied, the cytoscutes are covered with minute denticles. Nothing even remotely similar to this has been reported elsewhere, and this character underlines the morphological uniqueness of *Callistocilla* (Hoffman 1977)
- In the two studied Nearctic Xystodesmidae (*Gyalostethus monticolens* (Chamberlin, 1951) and *Sigmoria nigrimontis* (Chamberlin, 1947)) the margins of the otherwise normal cytoscutes are undulated.

Alternatively, the similarities in cuticle miscrosculpture might reflect similarities in habits. However, considering 1) our only fragmentary knowledge about the habits of these millipedes and 2) the modest number of taxa included in the present study, compared with the enormous diversity of Chelodesmidae and related families, the significance of these signals remains uncertain.

ACKNOWLEDGEMENTS

Particular thanks go to Thies Büscher (Univ. Kiel) for sharing his deep insight into cuticle microstructure and making many important suggestions; further thanks to Andy Sombke (Univ. Vienna), Louise Isager Ahl (NHMD), and the editors and referees for more useful suggestions, especially Leif Moritz who provided very comprehensive and constructive comments; and deep thanks to Slobodan Makarov, Dragan Antić and their team in Serbia for arranging the 20th International Congress of Myriapodology for which the present research was prepared.

REFERENCES

Akkari N, Enghoff H. 2011. On some surface structures of potential taxonomic importance in families of the suborders Polydesmidea and Dalodesmidea (Polydesmida, Diplopoda). Zookeys. 156:1–24. http://dx.doi.org/10.3897/zookeys.156.2134.

Anilkumar PA, Wesener T, Moritz L. 2022 First record of the order Polyzoniida from the Indian subcontinent with an integrative description of a new genus (Diplopoda, Colobognatha, Siphonotidae). Zootaxa. 5182(5):401–428. https://doi.org/10.11646/zootaxa.5182.5.1.

Bouzan RS, Iniesta LFM, Pena-Barbosa JPP and Brescovit AD. 2021. Six new species of the widespread Brazilian millipede genus *Eucampesmella* (Polydesmida: Chelodesmidae). Zoologia. 38:e66300. https://doi.org/10.38977/zoologia.38.e66300.

Bouzan RS, Means JC, Ivanov K, Ferreira RL, Brescovit AD, Iniesta LFM. 2022. Worldwide distribution of cave-dwelling Chelodesmidae (Diplopoda, Polydesmida). International Journal of Speleology. 51(3):235–248. https://doi.org/10.5038/1827-806X.51.3.2448.

Büscher TH, Kryuchkov M, Katanaev VL, Gorb SN. 2018. Versatility of Turing patterns potentiates rapid evolution in tarsal attachment microstructures of stick and leaf insects (Phasmatodea). Journal of the Royal Society Interface. 15(143):20180281. https://doi.org/10.1098/rsif.2018.0281.

Edgecombe GD, Giribet G. 2006. A century later – a total evidence re-evaluation of the phylogeny of scutigeromorph centipedes

(Myriapoda:Chilopoda). Invertebrate Systematics. 2006(20):503–525. https://doi.org/10.1071/IS05044.

Eisenbeis G, Wichard W. 1985. Atlas zur Biologie der Bodenarthropoden. Stuttgart, New York: Gustav Fischer Verlag.

Enghoff H. 2014. A mountain of millipedes I: An endemic species-group of the genus *Chaleponcus* Attems, 1914, from the Udzungwa Mountains, Tanzania (Diplopoda, Spirostreptida, Odontopygidae). European Journal of Taxonomy. 100:1–75. http://dx.doi.org/10.5852/ejt.2014.100

Enghoff H. 2017. A new East African genus of spirostreptid millipedes (Diplopoda, Spirostreptida, Spirostreptidae), with notes on their fungal ectoparasite *Rickia gigas*. Zootaxa. 4273(4):501–530. https://doi.org/10.11646/zootaxa.4273.4.3.

Enghoff H. 2018. A mountain of millipedes VI. New records, new species, a new genus, and a general discussion of Odontopygidae from the Udzungwa Mts, Tanzania (Diplopoda, Spirostreptida, Odontopygidae). European Journal of Taxonomy. 394:1–29. https://doi.org/10.5852/ejt.2018.394.

Enghoff H. 2022. A mountain of millipedes X. Species of Pyrgodesmidae and Cryptodesmidae in the Udzungwa Mountains, Tanzania (Diplopoda, Polydesmida). European Journal of Taxonomy. 845:66–100. https://doi.org/10.5852/ejt.2022.845.1955.

Enghoff H, Reboleira ASPS. 2017. Diversity of non-Laboulbenialean fungi on millipedes. Studies in Fungi 2(1):130–137. http://www.studiesinfungi.org/pdf/SIF_2_1_15.pdf

Enghoff H, Ngute ASK, Mnendendo HR Kivambe, EE, Mhagawale W, Malanda RC, Mpoto A, Marshall AR 2025. A mountain of millipedes XII. The Chelodesmidae of the Udzungwa Mountains, Tanzania (Diplopoda, Polydesmida). European Journal of Taxonomy. 997:210–255. https://doi.org/10.5852/ejt.2025.997.2935.

Frederiksen SB, Enghoff H. 2015. East African odontopygid millipedes 4: A restricted redefinition of the genus *Rhamphidarpoides* Kraus, 1960, a related new genus, five new species, and notes on solenomere function (Diplopoda; Spirostreptida; Odontopygidae). Zootaxa. 3926:541–560. http://dx.doi.org/10.11646/zootaxa.3926.4.5.

Fusco G, Brena C, Minelli A 2000. Cellular processes in the growth of lithobiomorph centipedes (Chilopoda: Lithobiomorpha). A cuticular view. Zoologischer Anzeiger. 239:91–102.

Golovatch SI, Enghoff H, Efeykin BD. 2025 *Chondrodesmus riparius* Carl, 1914, a millipede species new to the fauna of Costa Rica, originally described from Colombia, and introduced to and presently widespread across Europe (Diplopoda, Polydesmida, Chelodesmidae). Zootaxa. 5692(1):161–174. https://doi.org/10.11646/zootaxa.5692.1.8.

Güerri-Agulló B, Gómez-Vidal S, Asensio L, Barranco P, Lopez-Llorca LV. 2010. Infection of the Red Palm Weevil (*Rhynchophorus ferrugineus*) by the entomopathogenic fungus *Beauveria bassiana*: A SEM Study. Microscopy Research and Technique. 73:714–725.

Hannibal JT, May WJ. 2021. Permian millipedes from the Fort Sill fissures of southwestern Oklahoma, with comments on allied taxa and millipedes preserved in karstic environments. Journal of Paleontology. 95(3):586-600. https://doi.org/10.1017/jpa.2020.100.

Hoffman RL 1977. East African prepodesmid millipedes. Revue de Zoologie africaine. 91(1):69–82.

Liu S, Jobert F, Rahneshan Z, Doyle SM, Rober S. 2021. Solving the puzzle of shape regulation in plant epidermal pavement cells. Annual Review of Plant Biology. 72:525–550.

Manton SM. 1977. The Arthropoda. Habits, functional morphology and evolution. Oxford: Clarendon Press.

Marek PE, Krejca JK, Shear WA. 2016. A new species of *Illacme* Cook & Loomis, 1928 from Sequoia National Park, California, with a world catalog of the Siphonorhinidae (Diplopoda, Siphonophorida). Zookeys. 626:1–43.

Mauriès JP, Geoffroy J-J. 2000. Nouvelle description, classification, répartition et variations morphologiques inter-populations d'un diplopode troglobie du sud-est du Brésil (Diplopoda, Polydesmida, Chelodesmidae). Zoosystema. 22(1):153–168

Moretto M, Minelli A, Fusco G. 2015. Cell size versus body size in geophilomorph centipedes. The Science of Nature. 102:16 http://dx.doi.org/10.1007/s00114-015-1269-4.

Moritz L, Parra-Gómez A. 2023. *Notorhinus floresi* sp. nov. gen. nov.: The first records of Siphonophorida in Chile and Siphonorhinidae in South America (Colobognatha). Arthropod Systematics and Phylogeny. 81:565–579. https://doi.org/10.3897/asp.81.e100520.

Moritz L, Gregory SJ, Wesener T. 2022. A pinhead millipede astray: a new polyzoniidan millipede from New Zealand in Great Britain and the genus *Siphonethus* Chamberlin, 19220 in New Zealand (Polyzoniida: Siphonotidae). New Zealand Entomologist. 44(2):88–120. https://doi.org/10.1080/00779962.2022.20.

Muntoreanu TG, da Silva Cruz R, Melo-de-Pinna GF 2011. Comparative leaf anatomy and morphology of some neotropical Rutaceae: *Pilocarpus* Vahl and related genera. Plant Systematics and Evolution. 296:87–99.

Nickerl J, Helbig R, Schulz H-J, Werner C, Neinhuis C. 2013. Diversity and potential correlations to the function of Collembola cuticle structures. Zoomorphology. 132:183–195. http://dx.doi.org/10.1007/s00435-012-0181-0.

Pena-Barbosa JPP, Sierwald P, Brescovit AD. 2013. On the largest chelodesmid millipedes: taxonomic review and cladistic analysis of the genus *Odontopeltis* Pocock, 1894 (Diplopoda; Polydesmida; Chelodesmidae). Zoological Journal of the Linnean Society. 169:737–764.

Reboleira ASPS, Enghoff H 2015. Redescription of *Lusitanipus alternans* (Verhoeff, 1893) (Diplopoda, Callipoda, Dorypetalidae) and ecological data on its Laboulbeniales ectoparasites in caves. Zootaxa. 395(5):567–576. http://dx.doi.org/10.11646/zootaxa.3957.5.5.

Reboleira ASPS, Hosseini MJM, Sadeghi S, Enghoff H. 2015. Highly disjunct and highly infected millipedes – a new cave-dwelling species of *Chirazziulus* (Diplopoda: Spirostreptida: Cambalidae) from Iran and notes on Laboulbeniales ectoparasites. European Journal of Taxonomy. 146:1–18. http://dx.doi.org/10.5852/ejt.2015.146.

Rebora M, Salerno G, Piersanti S, Saitta V, Venturi DM, Li C, Gorb S. 2023. The armoured cuticle of the black soldier fly *Hermetia illucens*. Scientific Reports. 13:22101. https://doi.org/10.1038/s41598-023-49549-5.

Recuero E, López-Strada EK, Harden CW. 2026. Insights on the enigmatic millipede order Siphoniulida (Myriapoda, Diplopoda): a new species bearing ozopores and its phylogenetic implications. PeerJ. 14:e20594. https://doi.org/10.7717/peerj.20594.

Shear WA. 1977. Millipeds (Diplopoda) from caves in Mexico, Belize and Guatemala. III. Accademia Nazionale dei Lincei, Problemi Attuali di Scienza e di Cultura. 171(3):235–265.

Shear WA, Ferreira RL, Iniesta LFM, Marek P. 2016. A millipede missing link: Dobrodesmidae, a remarkable new polydesmidan millipede family from Brazil with supernumerary rings (Diplopoda, Polydesmida), and the establishment of a new suborder Dobrodesmidea. Zootaxa. 4178(3):371–390 http://www.mapress.com/j/zt/.

Stoev P, Akkari N, Komerički A, Edgecombe GD, Bonato L. 2015. At the end of the rope: *Geophilus hadesi* sp. n. – the world's deepest cave-dwelling centipede (Chilopoda, Geophilomorpha, Geophilidae). In: Tuf IH, Tajovský K, editors. Proceedings of the 16th International Congress of Myriapodology, Olomouc, Czech Republic. ZooKeys. 510:95–114. https://dx.doi.org/10.3897/zookeys.510.961.