REASSESSMENT OF *GYRAULUS* SPP. (GASTROPODA, PLANORBIDAE) FROM THE MIDDLE MIOCENE OF NÖRDLINGER RIES, GERMANY

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Abstract *Several fossil species of* Gyraulus *(Gastropoda: Hygrophila: Planorbidae) are known from the Miocene of continental Europe. An unpublished doctoral thesis from Bolten (1977) brought to light some new records of species from the Middle Miocene of Nördlinger Ries in southern Germany:* G. ludovici *(Noulet, 1854),* G. kleini *Gottschick & Wenz, 1916 and* G. oxystoma *(Klein, 1846). As the latter is considered one of the last in a lineage of endemics from the supposedly contemporaneous Lake Steinheim (Steinheim am Albuch), this report caught our attention. Thus, we re-analysed Bolten's original material, arguing here that his* Gyraulus *spp. were misidentified: all his specimens belong to another common (and morphologically variable) Early/Middle Miocene species:* G. applanatus *(Thomä, 1845). Finally,* G. kleini *is here synonymised with* G. applanatus.

Key words Gyraulus, *Hygrophila, Lake Steinheim, pulmonates, Ries impact crater.*

INTRODUCTION

The Middle Miocene impact crater at Nördlinger Ries, southern Germany, is considered one of the best-preserved impact structures on Earth (Pohl *et al*., 1977; Hüttner & Schmidt-Kaler, 1999; Sturm *et al*., 2013). Recent dating reported an age of 14.808±0.038 Ma for the Ries impact (Schmieder *et al*., 2018). The locality is known for well-preserved plant and vertebrate fossils (Weber, 1941; Dehm *et al*., 1977; Heizmann & Fahlbusch, 1983); the mollusks, however, have not been subject to much attention since the early 20th century (Wenz, 1923, 1924; Dehm *et al*., 1977).

The unpublished doctoral thesis of Bolten (1977) brought to light some fossil gastropods from Nördlinger Ries. Such works, even though unpublished, still remain a valuable (and sometimes the only) source of information on several aspects of Germany's fossil outcrops and their fauna and flora. Among the mollusks reported by Bolten (1977), he identified three species belonging to the planorbid genus *Gyraulus* Charpentier, 1837, namely: *G. ludovici* (Noulet, 1854), *G. kleini* Gottschick & Wenz, 1916, and *G. oxystoma* (Klein, 1846). Despite the first two forms being commonly reported from other Miocene outcrops, the latter is a species that has been considered endemic to the Miocene Lake Steinheim, SW Germany, which supposedly formed concomitantly to the Steinheim Basin (Mensink, 1984; Gorthner & Maier-Brook, 1985; Höltke & Rasser, 2017).

The Steinheim planorbid snails are a textbook example of endemic intralacustrine speciation and evolution. Starting with *G. kleini* in the basal strata, the *Gyraulus* lineage in Steinheim quickly diversified into several endemic forms, of which one of the latest to appear was *G. oxystoma* (Gorthner & Meier-Brook, 1985; Rasser, 2013a, 2013b). Bolten's (1977) thesis is the only report of a supposedly endemic *Gyraulus* species from outside Steinheim Basin. Previous reports of *Gyraulus* from Nördlinger Ries only mentioned *G. kleini* (Wenz, 1923, 1924; Seemann, 1941; Dehm *et al*., 1977); Dehm *et al.* (1977) also listed a *Gyraulus* cf. *albertanus* (Clessin, 1877).

As such, the occurrence of *G. oxystoma* in Nördlinger Ries (Bolten, 1977) brings up some questions and distinct possibilities: (1) *G. oxystoma* could have dispersed from Steinheim to Nördlinger Ries or vice-versa. (2) The so-called *G. oxystoma* from Nördlinger Ries is actually an endemic species, convergent in form to the actual species from Steinheim. (3) The so-called *G. oxystoma* from Nördlinger Ries was actually misidentified and the specimens belong to another Miocene species.

Bolten (1977) neither provided a thorough discussion of taxonomically relevant characters of his *Gyraulus* specimens nor meaningful comparisons with coeval forms; furthermore, he did

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not provide any figures. Therefore, our goal was to investigate this matter further, re-analyzing Bolten's original material. We have reassessed the taxonomy of Bolten's *Gyraulus* specimens from Nördlinger Ries, including not only his "*G. oxystoma*", but also the other two species previously mentioned. To that end, we also reassessed the taxonomic status of *G. kleini*.

Material and methods

The voucher material of Bolten (1977) is housed in the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG; Munich, Germany). All his specimens of *Gyraulus* spp. were analysed in the present work: BSPG 1956 I 233 (1 spc); BSPG 1956 I 609 (4 spc); BSPG 1959 I 22a (7 spc); BSPG 1959 I 22b (~50 spc); BSPG 1959 I 258 (15 spc); BSPG 1977 XIII (1 spc); BSPG 1977 XIII 95 (~20 spc); BSPG 1977 XIII 96 (1 spc); BSPG 1977 XIII 97 (~30 spc); BSPG 1977 XIII 98 (1 spc); BSPG 1977 XIII 99 (6 spc); BSPG 1977 XIII 100 (7 spc); BSPG 1977 XIII 101 (~25 spc); BSPG 1977 XIII 102 (1 spc); BSPG 1977 XIII 103 (13 spc); BSPG 1977 XIII 104 (3 spc); BSPG 1977 XIII 105 (4 spc); BSPG 1977 XIII 107 (4 spc); BSPG 1977 XIII 108 (2 spc); BSPG 1977 XIII 109 (3 spc); BSPG 1977 XIII 110 (~25 spc); BSPG 1977 XIII 112 (5 spc); BSPG 1977 XIII 113 (~40 spc).

Comparative material of *Gyraulus* spp. used in the present study is deposited in the collections of the BSPG, the Department of Geosciences of the Eberhard Karls Universität Tübingen (GPIT, Tübingen, Germany; formerly "Geologisch-Paläontologisches Institut Tübingen"), the micropaleontology collection of the Bayerisches Landesamt für Umwelt (LfU; Munich, Germany), and the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany). The latter counts with a vast collection of specimens from Steinheim (including type material; Salvador *et al*., 2016a). Additional data were gathered from the literature.

Results and Discussion

In the first place, we present a brief discussion on each of the three species (*G. oxystoma*, *G. ludovici* and *G. kleini*), including information on their diagnostic characters. This is followed by a brief discussion on a fourth species, *G. applanatus* (Thomä, 1845), which is important for the reassessment of Bolten's *Gyraulus* spp. from Nördlinger Ries that is presented afterwards.

***Gyraulus oxystoma* (Klein, 1846):** This species was originally described from Steinheim; its type specimen(s) is lost (Salvador *et al*., 2016a). It is thought to belong to a lineage endemic to Lake Steinheim that started with *G. kleini* (Rasser, 2013b).

Gyraulus oxystoma displays a unique morphology among German Miocene fossils (Fig. 1): it

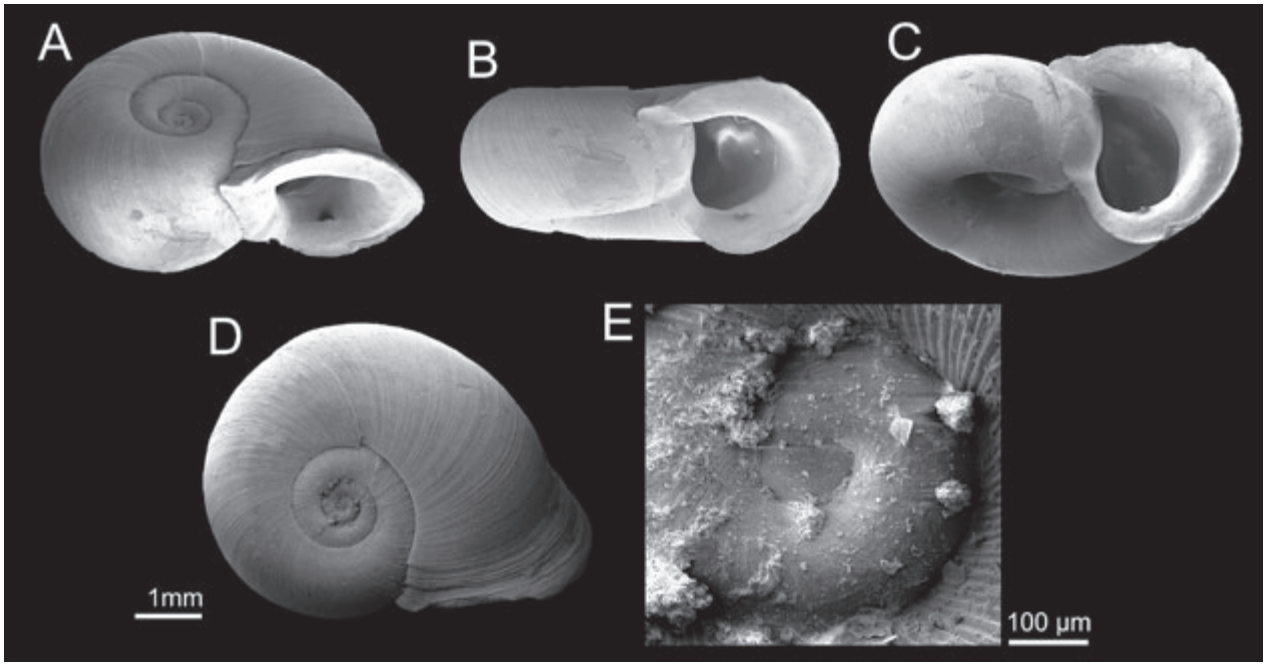

Figure 1 *Gyraulus oxystoma*, from type locality (Steinheim am Albuch), SMNS unnumbered (ex Jooss colln.).

has a relatively large shell (in comparison with most congeners), with round and very inflated whorls; the protoconch sculpture consists of several (ca. 20) spiral striae (Fig. 1E); the teleoconch sculpture consists of strongly marked growth lines resulting in a fine rib-like pattern; the aperture is D-shaped, with a strongly thickened and reflexed peristome.

***Gyraulus ludovici* (Noulet, 1854):** This species was first described from the Middle Miocene of Sansan, France. It has been long considered a subspecies of *G. applanatus* (*e.g.*, Wenz, 1923), but is now considered a distinct species due to its larger size, the whorls being more closely packed together, and the presence of a more distinct (keel-like) central angulation (Fischer, 2000; Harzhauser *et al*., 2014b). Previous reports of *G. ludovici* from Germany (*e.g.*, Gall, 1972) were recently reclassified as *G. applanatus* (*e.g.*, Salvador & Rasser, 2014).

***Gyraulus kleini* (Gottschick & Wenz, 1916):** This species was first described as *Planorbis laevis* Klein, 1846 (:79, pl. 1, fig. 26a–c) [*non* Alder, 1838], which was a preoccupied name. Thus, it was later given the new name *Gyraulus multiformis kleini* Gottschick & Wenz, 1916 (:101, fig. 3). The species stems from the Upper Freshwater Molasse (abbreviated OSM, from the German "Oberen Süßwassermolasse") of southern Germany (zone MN5); its type localities are Dächingen and Hohenmemmingen (Salvador *et al*., 2016a; syntypes SMNS 25263/2005, 2 specimens, Figs 2I–J).

Gottschick & Wenz (1916) already noted in their material that *G. kleini* and two other species occurring in Hohenmemmingen, *G. applanatus* and *G. dealbatus* (Braun, 1851), showed a gradation of forms among themselves. The specimens usually identified as either *G. kleini* or *G. dealbatus* in the literature present higher and more inflated shells, with a more rounded body whorl profile (there is a faint angulation on the whorl's median portion), rapidly growing whorls and a more rounded aperture (Figs 2A–D; *e.g.*, Gottschick & Wenz, 1916; Kowalke & Reichenbacher, 2005; Salvador & Rasser, 2014). *Gyraulus applanatus*, on the other hand, has a flattened shell, with the whorls increasing more slowly (and regularly) in size, a better marked angulation on the laterobasal portion of the body whorl and a more pointed arrowhead-like aperture (Figs 2F–H, K–L; Gottschick & Wenz, 1916; Kowalke & Reichenbacher 2005; Salvador & Rasser, 2014). Curiously, however, the type specimens of *G. kleini*, recently brought to light by Salvador *et al*. (2016a: pl. 5, fig. 16; reproduced here as Figs 2I–J), are more similar to *G. applanatus* rather than to *G. dealbatus*.

The presence of a continuum of morphological variation between *G. dealbatus* and *G. applanatus* led Kowalke & Reichenbacher (2005) to synonymise the two species: the older valid name is *G. applanatus*. This decision was followed by later authors working with equally variable fossils from other localities in Germany (*e.g.*, Salvador *et al*., 2016b), but it has not been fully embraced by researchers working on more eastern European localities (*e.g.*, Harzhauser *et al*., 2014a, 2014b) where the full spectrum of conchological variability has not been observed.

Nevertheless, the validity of *G. kleini* was not fully examined by Kowalke & Reichenbacher (2005). The species has been considered distinct in the literature, although Salvador *et al*. (2017), studying scarce material from the type locality, alluded to the possibility of if being synonymous with *G. applanatus*. Herein, with material from several localities (including specimens from the study of Salvador *et al*., 2017) and thus, the full breath of morphological variation (Fig. 2), as well as access to the type specimens of *G. kleini* (Figs 2I–J), we propose that *G. kleini* should be considered synonymous with *G. applanatus*.

Gyraulus kleini is also reported from the basal layers of Steinheim and there it is considered to have given rise to a lineage of endemic species (Rasser, 2013a, 2013b). Curiously, Finger (1998) reported that only the form *G. kleini* is found in the basal layers of Steinheim and that both *G. applanatus* and *G. dealbatus* are absent; her figures, however, seem to show the whole span of variation typical of *G. applanatus*. The identity of Steinheim's *G. kleini* will be further investigated elsewhere.

***Gyraulus applanatus* (Thomä, 1845):** The type localities of this species are Wiesbaden and Mainz-Weisenau (Thomä, 1845). Overall, this is a common species in the Miocene of Central Europe, with some possible records from the Late Oligocene (Chattian) (Wenz, 1923; Kowalke & Reichenbacher, 2005; Höltke *et al*., 2018). As explained above, the shells show a considerable amount of morphological variation, with extreme forms described as distinct species, but with a continuum of intermediates linking them (Fig. 2;

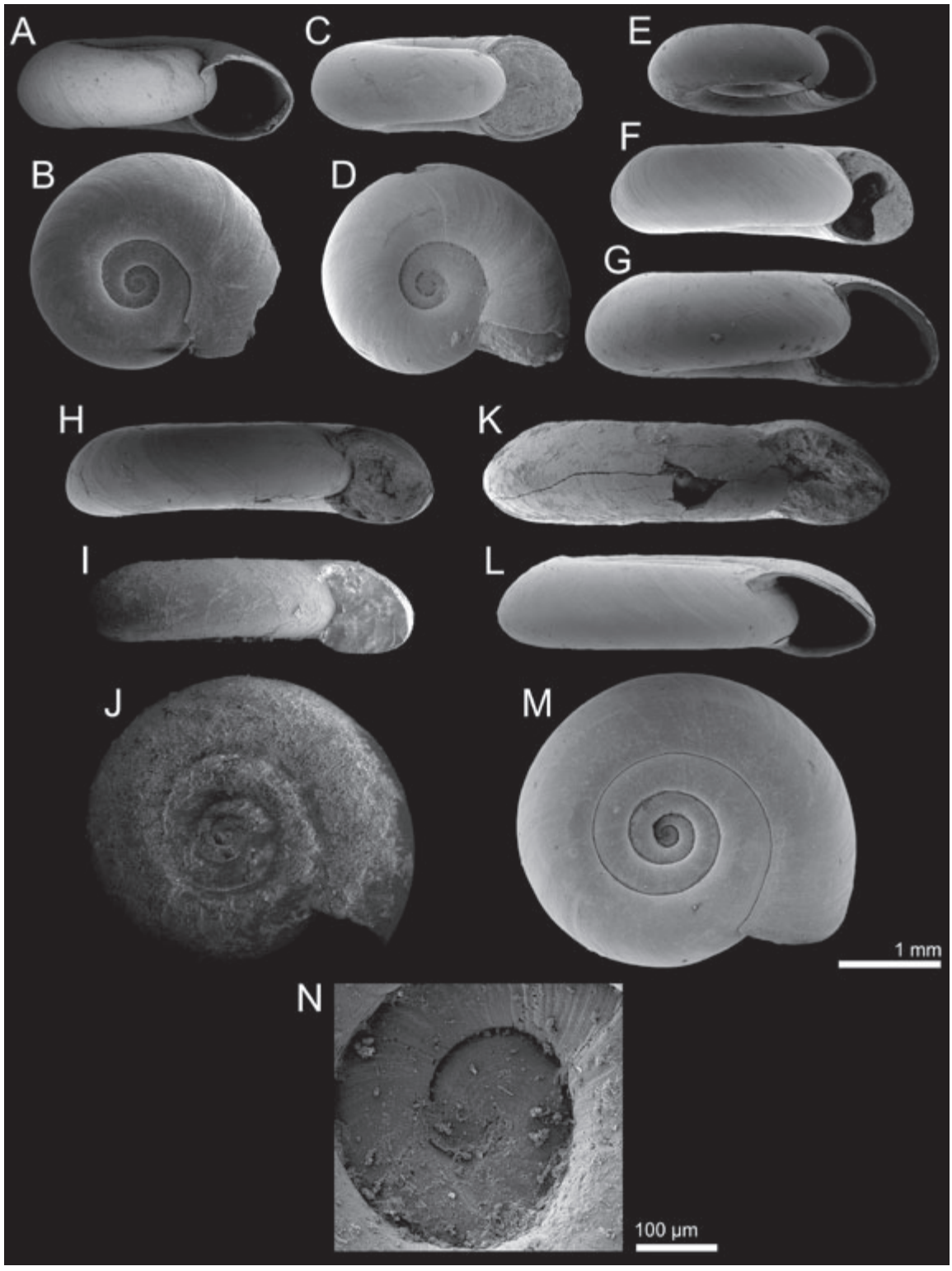

Figure 2 *Gyraulus applanatus*, from several outcrops of the Early/Middle Miocene of southern Germany. **A** BSPG 1959 II 18030, spc #1, from Sandelzhausen (OSM). **B** BSPG 1959 II 18030, spc #2, from Sandelzhausen (OSM). **C–D** BSPG 1959 II 18020, from Sandelzhausen (OSM). **E** LfU-SPR2014-035, from Buttenwiesen (OBM, Kirchberg Formation). **F** BSPG 1959 II 18045, from Sandelzhausen (OSM). **G** SMNS 68654, spc #1, from Oggenhausen (OSM). **H** BSPG 1959 II 18047, spc #1, from Sandelzhausen (OSM). **I–J.** SMNS 25263/2005, syntype of *G. kleini*, from Hohenmemmingen or Dächingen (OSM). **K** SMNS 107330, from Hohenmemmingen (OSM). **L.** SMNS 68654, spc #2, from Oggenhausen (OSM). **M** SMNS 68654, spc #3, from Oggenhausen (OSM). **N** BSPG 1959 II 18047, spc #2, from Sandelzhausen (OSM).

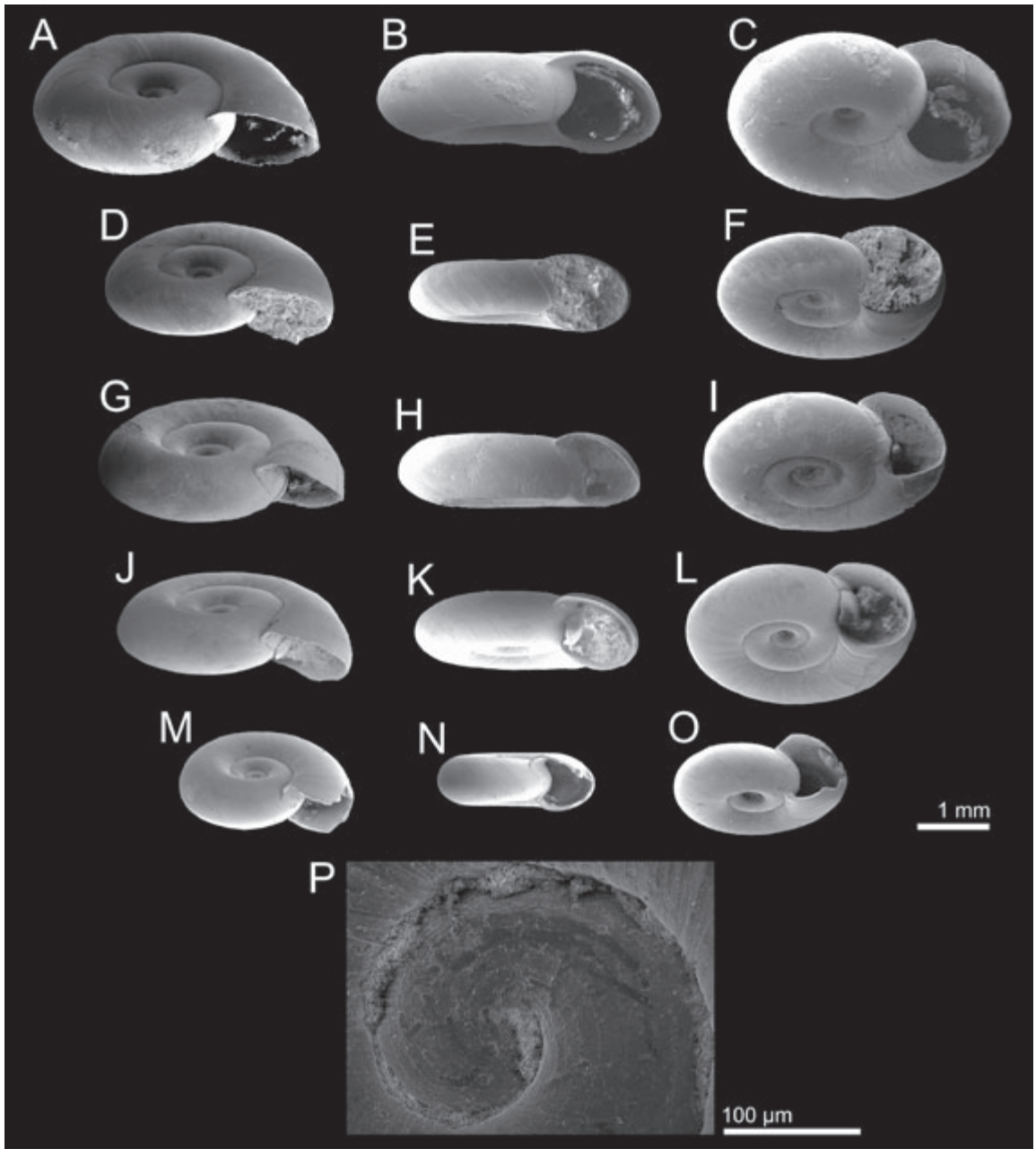

Figure 3 *Gyraulus applanatus*, voucher material of Bolten (1977). **A–F** Specimens identified as *G. oxystoma* by Bolten (1977). **A–C** BSPG 1977 XIII 95. **D–F** BSPG 1977 XIII 97. **G–I** Specimens identified as *G. ludovici* by Bolten (1977), BSPG 1977 XIII 100. **J–P** Specimens identified as *G. kleini* by Bolten (1977). **J–L** BSPG 1977 XIII 101. **M–P** BSPG 1977 XIII 111.

see also Kowalke & Reichenbacher, 2005). This has been reported for multiple localities of the Upper Brackish Molasse (abbreviated OBM, from the German "Oberen Brackwassermolasse") and OSM (*e.g.*, Gottschick & Wenz, 1916; Kowalke & Reichenbacher, 2005; Salvador & Rasser, 2014; Salvador *et al.*, 2016b, 2017).

Bolten's *Gyraulus* spp.: From the 25 lots that compose the *Gyraulus* spp. voucher material of Bolten (1977), most were identified by him as *G. kleini*; only three were identified as *G. oxystoma* and another three as *G. ludovici*. All of Bolten's (1977) voucher specimens (Fig. 3) fall well within the range of conchological variation seen in *G. applanatus*: size, number of whorls, overall shell shape, aperture shape, positioning and strength of whorl angulation, and protoconch sculpture.

Bolten's "*G. kleini*" mostly represent the intermediate form of *G. applanatus* (Figs 3J–P), while

his other two "species" represent more extremes forms in the morphological continuum of variation of *G. applanatus*. Bolten's "*G. oxystoma*" represents the highest and more inflated shells (usually referred to *G. dealbatus*; Figs 3A–F), while his "*G. ludovici*" represents the most flattened shell profiles (the typical *G. applanatus*; Figs 3G–I).

Finally, H. Gall *in* Dehm *et al*. (1977) listed a possible *G.* cf. *albertanus* from Nördlinger Ries, but did not illustrate it. Gall stated that the material he used is the same as Bolten's (1977) in the BSPG collection, but there is no mention of a precise catalog number; neither there was a clear label indicating the material analysed by Gall. However, the fact that Bolten (1977) had access to the same specimens mean that he identified them as something else. *Gyraulus albertanus* was originally described from the nearby locality of Undorf (MN5) and is easily diagnosable by its larger and more inflated shell (Salvador & Rasser, 2014). Given this shell morphology, it is tempting to conclude that these specimens were those Bolten (1977) identified as *G. oxystoma*, but it is impossible to be certain. In any event, it is safe to assume *G. albertanus* did not occur in Nördlinger Ries.

Conclusions

Gyraulus kleini is here considered synonymous with *G. applanatus; G. dealbatus* likewise remains a synonym of *G. applanatus*. The only representative of *Gyraulus* in Nördlinger Ries is thus *G. applanatus*, which is a ubiquitous form in the Early/Middle Miocene of the North Alpine Foreland Basin and its adjacent areas. As such, *G. ludovici* and *G. oxystoma* are absent from sediments of Nördlinger Ries. The latter species remains endemic to the Steinheim Basin.

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